National Library of Canada
Bibliothèque nationale du Canada

Canadian Theses Service
Services des thèses canadiennes

Ottawa, Canada
K1A 0N4

CANADIAN THESES

THÈSES CANADIENNES

NOTICE

The quality of this microfiche is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us an inferior photocopy.

Previously copyrighted materials (journal articles, published tests, etc.) are not filmed.

Reproduction in full or in part of this film is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30. Please read the authorization forms which accompany this thesis.

AVIS

La qualité de cette microfiche dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de qualité inférieure.

Les documents qui font déjà l'objet d'un droit d'auteur (articles de revue, examens publiés, etc.) ne sont pas microfilmés.

La reproduction, même partielle, de ce microfilm est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30. Veuillez prendre connaissance des formules d'autorisation qui accompagnent cette thèse.

THIS DISSERTATION
HAS BEEN MICROFILMED
EXACTLY AS RECEIVED

LA THÈSE A ÉTÉ
MICROFILMÉE TELLE QUE
NOUS L'AVONS REÇUE

Canada

NL 339 (r. 86/01)

310

0-315-27041-1

National Library of Canada | Bibliothèque nationale du Canada

Canadian Theses Division | Division des thèses canadiennes

Ottawa, Canada
K1A 0N4

PERMISSION TO MICROFILM — AUTORISATION DE MICROFILMER

• Please print or type — Écrire en lettres moulées ou dactylographier

Full Name of Author — Nom complet de l'auteur

COLIN AUSTIN CHAPMAN

Date of Birth — Date de naissance

MAY 20 1959

Country of Birth — Lieu de naissance

CANADA

Permanent Address — Résidence fixe

307 10159 118 ST

Title of Thesis — Titre de la thèse

BEHAVIOURAL ECOLOGY OF THE ST. KITTS VERVET

University — Université

UNIVERSITY OF ALBERTA

Degree for which thesis was presented — Grade pour lequel cette thèse fut présentée

MASTER OF ART

Year this degree conferred — Année d'obtention de ce grade

1983

Name of Supervisor — Nom du directeur de thèse

LINDA FEDIGAN

Permission is hereby granted to the NATIONAL LIBRARY OF CANADA to microfilm this thesis and to lend or sell copies of the film.

The author reserves other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's written permission.

L'autorisation est, par la présente, accordée à la BIBLIOTHÈQUE NATIONALE DU CANADA de microfilmer cette thèse et de prêter ou de vendre des exemplaires du film.

L'auteur se réserve les autres droits de publication; ni la thèse ni de longs extraits de celle-ci ne doivent être imprimés ou autrement reproduits sans l'autorisation écrite de l'auteur.

Date

JUNE 16 1983

Signature

C.A. Chapman

NL-91 (4/77)

THE UNIVERSITY OF ALBERTA

Behavioural Ecology of the St. Kitts Vervet

by

Colin A. Chapman

©

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF Master of Arts.

Department of Anthropology

Edmonton, Alberta

Fall 1983

THE UNIVERSITY OF ALBERTA

RELEASE FORM

NAME OF AUTHOR Colin A. Chapman

TITLE OF THESIS Behavioural Ecology of the St. Kitts Vervet

DEGREE FOR WHICH THESIS WAS PRESENTED Master of Arts.

YEAR THIS DEGREE GRANTED Fall 1983

Permission is hereby granted to THE UNIVERSITY OF ALBERTA LIBRARY to reproduce single copies of this thesis and to lend or sell such copies for private, scholarly or scientific research purposes only.

The author reserves other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's written permission.

(SIGNED) C. A. Chapman

PERMANENT ADDRESS:

#307 10159 118 ST

EDMONTON, ALBERTA

CANADA

DATED June 16 1983

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Behavioural Ecology of the St. Kitts Vervet submitted by Colin A. Chapman in partial fulfilment of the requirements for the degree of Master in Art.

Linda Marie Fedigan

Supervisor

Date April 27 1983

Abstract

The relationships between specific ecological variables and the expression of behaviours were investigated in a group of vervet monkeys (Cercopithecus aethiops) inhabiting an ecologically diverse home range on the dry savanna-like peninsula of St. Kitts, West Indies. The study group's behaviour was shown to vary between areas which had different values on four factors produced from a factor analysis of 20 ecological variables.

A number of relationships between behaviour and ecology were found that have not been previously described; for instance it was found that attentive behaviours were negatively related to cover, while social behaviours were positively related, also agonistic behaviours and affiliative behaviours were positively related to food abundance. Open areas with edge proved to be important to the group and a number of behaviours were expressed for longer durations, and/or more frequently in these areas.

As shown by censusing the population density of the vervets in different habitats, the vervets of the study group were selecting habitats, preferring areas of secondary growth. Comparisons of this study with others, illustrates a need to carefully examine behavioural ecological relationships using a quantitative methodology.

Acknowledgements

I would like to express my appreciation to Drs. Linda Fedigan and Laurence Fedigan whose interest, assistance and encouragement made this study possible. I would also like to express my gratitude to Peter Clark, whose assistance in the field was invaluable. Lastly, I would like to thank Dr. John Addicott and Dr. Owen Beattie for advice and assistance during the final stages of this work. This work was supported by a NSERC Postgraduate Research Grant No. 5574219.

Table of Contents

Chapter		Page
I.	INTRODUCTION	1
	A. Related Studies	3
II.	METHODS	9
	A. Site Description	9
	B. Behavioural Sampling	11
	C. Ecological Sampling	13
III.	GENERAL DESCRIPTION OF THE ECOLOGY OF THE STUDY GROUP	20
	A. Ranging Behaviour	20
	B. Sleeping Site	23
	C. Daily Pattern	24
	D. Feeding Ecology	31
	E. Interrelationships Between the Ecological Variables	37
IV.	BEHAVIOURAL ECOLOGICAL RELATIONSHIPS	41
V.	DIFFERENTIAL RANGE USE	53
VI.	DISCUSSION	60
VII.	BIBLIOGRAPHY	66
VIII.	Appendix 1 : Ethogram of Vervet Behaviour	74
IX.	Appendix 2 : Study Area of the St. Kitts Vervet	83
X.	Appendix 3 : The Plants Found on Sir Timothy Hill, St. Kitts	84

LIST OF TABLES

Table — Page

Table 1: Population estimates of the groups of vervet monkey (Cercopithecus aethiops) on Sir Timothy Hill, St. Kitts, 1972 (McGuire 1974) and 1982 (Fedigan unpublished) 10

Table 2: Ecological variables examined 15

Table 3: The composition of the diet of the vervet monkey (Cercopithecus aethiops) study group, St. Kitts. (Based on observed feeding frequencies) 32

Table 4: The frequency of use of the available plant parts by the vervet monkey (Cercopithecus aethiops) study group, St. Kitts 34

Table 5: The four major ecological factors, listing those variables with high loadings. (% of the variance in the ecological variables they explain) 39

Table 6:

F Test values examining the relationships between factors and behaviours 50

Table 7:

Correlation values describing the relationship between factors and behaviours 51

LIST OF FIGURES

Figure Page

Figure 1:
The diurnal distribution of the average number of minutes per hour that any individual vervet monkey in the St. Kitts study group was observed to be feeding 25

Figure 2:
The diurnal distribution of the average number of minutes per hour that any individual vervet monkey in the St. Kitts study group was observed to be locomoting 26

Figure 3:
The diurnal distribution of the average number of minutes per hour that any individual vervet monkey in the St. Kitts study group was observed to be playing 27

Figure 4:
The diurnal distribution of the average number of minutes per hour that any individual vervet monkey in the St. Kitts study group was observed to be resting 28

Figure 5:

The diurnal distribution of the average number of minutes per hour that any individual vervet monkey in the St. Kitts study group was observed to be grooming..... 29

Figure 6:

The % of the total number of monkeys seen on the different transects..... 54

I. INTRODUCTION

Chapter 1

Early in the history of modern primate field studies researchers became interested in the question of how the ecological conditions experienced by a primate social group influenced its behaviour (Altmann, 1959; DeVore, 1963; Hall, 1963; Chalmers, 1968; Gartlan, 1968). It is extremely common to find references in the primate literature which make claims relating observed behavioural traits to ecological conditions (DeVore, 1963; Crook, 1970; Eisenberg et al., 1972; Jorde and Spuhler; 1974). For example, patterns of ranging behaviour have been related to ecological conditions, such as the abundance and distribution of food resources. In addition to behaviours which directly relate to the animal's environment, such as ranging behaviours, and foraging patterns, arguments have been advanced in which such behaviours as play and grooming are related to the ecological conditions experienced by the animal. These claims are so commonly found in the primate literature that many of the relationships described are considered established fact. However, there has often been general acceptance of described relationships without sufficent support. Only a handful of studies have attempted to examine these hypothesized relationships between behaviour and ecology quantitatively and systematically. It is not uncommon to find theoretical explanations of a species behaviour based upon relatively poorly investigated behavioural-ecological relationships.

The behaviours expressed by a group of primates must be generally appropriate for the environment in which they find themselves. The existence of specific relationships between some of the behaviours expressed by a social group of primates and selected aspects of the environment that they inhabit is the predictive model examined in this study. The objective of this research is to determine if consistent relationships between the analysed ecological conditions and the behaviours exhibited by the social group of primates under study can be validated statistically.

Many studies have been published recently that deal with aspects of feeding and ranging behaviour in primates, and that stress the analysis of

interspecific differences in feeding ecology (Altmann, 1974; Hladik, 1975, 1977; Struhsaker, 1978; Struhsaker and Leland, 1979; Milton, 1980). From such studies, attempts have been made to demonstrate that ecological variables have similar effects on phylogenetically diverse taxa (Eisenberg et al., 1972; Altmann, 1974; Jorde and Spuhler, 1974; Clutton-Brock and Harvey, 1977). Ecological variables, such as abundance of food or the availability of cover, are often suggested as causal factors of specified behaviours. Comparisons between studies and between species suffer oversimplification because such comparisons can consider only broad behavioural and ecological factors. Methodological differences between studies, and large interspecific variation limit validity of comparisons between behavioural and ecological factors (Clutton-Brock and Harvey, 1977). Comparisons between species are further restricted because not only are ecological factors influencing the behaviours, but also phylogeny sets inherent limits on behaviour. Thus, these analyses become confusing multivariate ones (Struhsaker, 1969; Gartlan, 1972; and Crook et al., 1976).

I would suggest that in order to determine relationships between specific behavioural and ecological variables, it will be more effective to compare different groups of the same species in distinctly different habitats. However, idiosyncratic differences in the behaviour of individuals in the groups may create high levels of behavioural variability between groups. This variability may not be related to ecological conditions, making behavioural ecological relationships difficult to demonstrate. In order to prevent this from biasing the analysis, observations on a large number of groups are normally required to obtain a satisfactory sample size for comparison. The need to obtain an adequate sample size severely limits the application of this approach. One possible solution is to examine behavioural changes within one social group as its members move between areas that express a range of ecological variables. This study is designed to take such an approach to the problem of how primate behaviour is influenced by specific ecological conditions.

This study examines how specific ecological variables, such as food density and diversity and cover, are associated with the behaviour of one group

of primates as it moves through it's home range. From an initial survey of Central America and the Caribbean in the summer of 1981, I selected the small Caribbean island of St. Kitts as the study site. Inhabiting St. Kitts is a population of vervet monkeys (Cercopithecus aethiops sabaeus), the ancestors of which were first introduced onto the island sometime in the 17th century (McGuire, 1974; Denham 1982a,b). A group of vervets living on the dry savanna-like peninsula of the island were selected as the study group because its ecologically diverse home range provides a wide range in the ecological variables. If any relationship existed between the ecological and behavioural variables, they should be apparent when extremes were compared. Cercopithecus aethiops is a good species for a study of this nature, for it is one of the most adaptable Cercopithecines (Struhsaker, 1969a; Kavanagh 1980). It is found not only in savanna habitats (Struhsaker, 1969a,1969b; Dunbar, 1974; Cheney, 1981), but also in mangrove swamps (Galat and Galat-Luong, 1976, 1977), rain forest (McGuire, 1974), farmland (Kavanagh, 1978a,b 1980a,b, 1981) and urban fringe areas (Krige and Lucas, 1974).

A. Related Studies

Although there is widespread acceptance of the idea that social behaviour is influenced by the ecological conditions experienced by a social group, there are few studies explicitly designed to analyse this in a quantitative manner. The most common approach used to examine the influence of ecology on behaviour is to compare different species (Crook and Gartlan, 1966; Struhsaker, 1969; Jorde and Spuhler, 1974; Spuhler and Jorde, 1975; Clutton-Brock and Harvey, 1977). There has been a plethora of studies which compare group parameters, such as population density, age/sex composition and home range size to various ecological variables. The most extensive research in this area is on ranging behaviour. DeVore (1963) was one of the first to discuss how the home range size of a primate group could be influenced by ecological variables such as food abundance and levels of predation. DeVore's interpretations were limited, because the majority of the field studies concluded by that time had been

carried out on terrestrial species. As more studies became available for comparison a large number of theoretical papers began to examine the relationship between ecology and primate social organizations (see; Crook and Gartlan, 1966; Kummer, 1967, 1971; Struhsaker, 1967; Aldrich-Blake, 1970; Denham 1971; Eisenberg et al., 1972; Clutton-Brock, 1974,1977; Hladik, 1975; Itani, 1977; Gaulin 1979). For example, Eisenberg et al. (1972) assigned various species to one of several "grades of social structure"; uni-male systems, age-graded systems, and multimale systems. Unimale systems favour arboreal, diurnal leaf-eaters, and the multimale system is a social structure specialized for intermediate sized terrestrial species. These researchers used various ecological conditions, such as degree of terrestriality or arboreality, intensity of predation and the abundance of food, as predictors of these grades. The major problem with these studies is the building of elaborate theoretical constructs on poorly researched systems.

The two most common ecological variables used to explain primate social behaviour are food abundance and predation levels. When comparing predation levels on different primate species, it has usually been assumed that "Life on the ground exposes a species to far more predation than does life in the trees" (DeVore, 1963:313). There has never been a study which has verified this. Depending upon the species being considered and on the defence strategy that it employs, predation can serve to increase or decrease dispersion. The most common strategy for predator avoidance involves cohesive group defence; only a few species use a strategy employing dispersion and concealment (Goss-Custard et al., 1972; Crook, 1972). Primate species employing both strategies utilize cover to either decrease the ease of predator detection, or to provide possible routes of escape. Fairbanks and Bird (1978) hypothesized that in forest dwelling primates increased levels of cover would decrease the need for cohesion, and they found that group cohesion was inversely related to cover. Earlier work by Struhsaker (1969) supports this hypothesis. Struhsaker found that where the level of cover was low there were few solitary animals in a population. The major problem with studies examining cover is that cover

has tended to be defined qualitatively. It has proven difficult to develop a measure which is appropriate to represent all the variety of different ways cover is utilized by primates.

Eisenberg et al. (1972) hypothesized that low food abundance results in large dispersed groups. Similarily, Crook and Gartlan (1966) and Kummer (1968) argued that the social organizations of species in which uni-male and all-male groups have the ability to form large aggregations reflects the adaptation to a low quality, seasonally arid environment. Species examples are gelada (Theropithecus gelada) and the hamadryas baboon (Papio hamadryas). Dunbar (1977) studied the gelada baboon and found that the herd tended to break up into more foraging units in poor habitats, while they foraged in larger groups in good habitats. Iwamato (1974) found contradictory evidence. He carried out a detailed comparison of the seasonal variation in the feeding behaviour of geladas and discovered that although the amount of grass decreases in the dry season, and the time spent feeding increases, uni-male groups do not seem to separate more frequently during the dry season than during the wet season.

Some authors have suggested that the frequency of certain behaviours is determined by the abundance of food resources. It has been posited that play, which is stated to require a "surplus" of energy, decreases when food becomes less available (Altmann, 1959; Loizos, 1966). Chalmers (1968) suggested that, since animals compete for food, there should exist a negative relationship with food abundance and the frequency of aggression. Hall (1963) suggested that when food is not abundant, more time must be spent foraging and this results in social behaviours, especially grooming, being expressed less frequently simply because of time constraints. Similar arguments have been advanced by Crook (1970) and Rowell (1972).

The abundance, distribution and quality of food resources have frequently been related to the amount and kind of territorial behaviour (Hamilton et al., 1975; Mitani and Rodman, 1979; Kavanagh, 1981). One theory suggests that territorial behaviour will be expressed when food resources are limited and defendable (Brown, 1964; Davies, 1978). In East Africa, Cheney (1981), Gartlan

and Brain (1968) and Struhsaker (1967a) all describe intense territorial defence, whereas in West Africa, Kavanagh (1981) noted territorial defence in some of the groups he studied but not in others. McGuire (1972) observed a general lack of territorial behaviour in the St. Kitts vervets he studied, although Poirer (1972), studying in different areas, reported territoriality.

One of the more adequately researched behavioural-ecological relationships examines how the spatial distribution of food resources influences patterns of group cohesion and dispersion (Crook, 1965; Gartlan and Brain, 1968; Crook, 1972; Crook et al., 1976). Studies examining this relationship from the availability of a broad range of evidence collected on other plant and animal interactions. Studies, such as Krebs (1978a) and Charnov (1976), have provided supporting evidence and mathematical models which demonstrate that as an animal's food resources become more "patchy", in either space or time, animals tend to alter foraging and social patterns appropriately. These studies help substantiate the claims that the dispersed group structure of spider monkeys (Ateles sp.) and chimpanzees (Pan sp.) are a response to patchy food resources (Gaulin, 1978; Klein and Klein, 1975; Nishida, 1968).

The abundance and distribution of food resources have been frequently evoked to explain a variety of behavioural states. For instance, as food abundance decreases the levels of grooming, play and affiliative behaviours are thought to decrease, while the level of agonism is viewed to increase. Also the level of dispersion that a group of primates exhibits is thought to be a function of the availability and dispersion of food resources. The amount of available cover and predator pressures are thought to influence dispersion, and by doing so they influence the expression of social behaviours.

Field observations have been carried out on the St. Kitts vervet since 1965, when Sade and Hildrech (1965) made a very general assessment of the distribution of monkeys on the island. Four years later, Poirier (1972) studied the general ecology and social behaviour of a number of groups on the island. In 1970, a 42 month study of the behaviour and ecology of a number of

different groups, located in various parts of the island, was initiated by McGuire (1974). The aim of this study was to compare the behaviour and the ecology of a number of different groups on the island, in an attempt to find consistent patterns. This study provides valuable insights, the most important of which is its illustration of the complexity of factors which influence the vervet's behaviour. Equally important, it illustrates the fact that these factors interact with each other. However, the problem of difficult and variable observation conditions, limit the actual value of the comparisons. Since the ecological variables outlined in McGuire's study were not defined and sampled in a replicable fashion and thus differ from those in this study, comparisons made between the studies are forced to be limited. Fairbanks and Bird (1978) and Fairbanks (unpublished) studied a single group of St. Kitts vervets and attempted to correlate some of the variation in the group's ranging behaviour to a number of ecological conditions. This study produced some interesting findings, however, they suffer from possible sampling bias of behaviours, which were collected ad libitum. As a consequence comparisons between the present study and Fairbanks and Bird's (1978) must be tentative.

Field studies done at different locations in Africa provide a wealth of comparative data. One of the earliest and most intensive studies on the vervet was carried out by Struhsaker (1966, 1967a,b, 1969) in the Amboseli Game Reserve, Kenya. The monkeys which Struhsaker studied inhabited the semi-arid savanna. Gartlan and Brain (1968) presented a description of the ecology and social behaviour of two groups of vervets in East Africa. One group inhabited an ecologically rich area which contained areas of semi-deciduous forest and grassland, while the other inhabited an ecologically poor savanna woodland area. Hall and Gartlan (1965) conducted a study which provides information on the ecology and behaviour of the vervet monkeys of Lolui Island, Lake Victoria. In addition to these studies, carried out on East African vervet populations, there are a number of studies on the West African vervet. Dunbar (1974) studied a population of vervet monkeys in Senegal which lived in the gallery forest along

the Oulou River. Galat and Galat-Luong (1976, 1977) presented ecological and behavioural data from two areas in Senegal. Both areas contain rich mangrove swamps. Three west African vervet monkey groups were studied by Kavanagh (1978a,b, 1980a,b, 1981). The three groups inhabitated distinctly different habitat types. They were found in thorn savanna, broadleaved savanna woodland, and farmland, and secondary forest. Investigations have also been carried out on vervet populations in South Africa. The groups studied inhabit a variety of ecological conditions (Basckin and Krige, 1973; Tollman and Simpson, 1975; Henzi and Lucas, 1980). The finding of these studies are not summarized here, as they are discussed where appropriate in the following chapters.

II. METHODS

Data for this study were collected during eight months of field observations on a wild group of vervet monkeys (Cercopithecus aethiops sabaeus) on the island of St. Kitts, West Indies. The vervets of St Kitts were introduced to the island from West Africa approximately 300 years ago (McGuire, 1974; Denham, 1982a,b). The population is still considered to be the same subspecies as its founding population in West Africa (Ashton, 1960). During the eight months in St. Kitts, over 1200 hours were spent at the study site and of this time 220 hours of actual focal animal data were collected.

This study was preceded by a ten month study of vervets in this area by Drs. Linda and Larry Fedigan. Their study was designed to census, by enumeration, the primate populations in the Timothy Hill area, and thus it provided this study with population estimates of the study groups and the neighboring groups. Their study also helped to habituate the vervets to the presence of a human observer. Since the same area was censused by McGuire (1974) between 1970 and 1972, it is possible to compare the population density of the groups on Timothy Hill over a ten year period. The population ten years ago and at present are presented in Table 1.

A. Site Description

Field observations were made on one group of vervet monkeys which inhabits a 200 meter high hill situated on the dry southeastern peninsula, known as Sir Timothy Hill. The group consisted of approximately 50 animals. The age/sex distribution of the group over the period of study averaged: 11 adult males, 2 subadult males, 19 adult females, 3 subadult females, 11 juveniles, and 3 infants. Over the eight months of the study five infants were born to the group, two of which subsequently died.

The group's home range contains a number of distinct habitat types, which are all used by the monkeys. The majority of the hill is a dry fire affected community, which is dominated by acacia (Acacia farnesiana), cacti, such as Melocactus intortus, Opuntia megeantha, and Cephalocereus royenii, and Agave

Table 1: Population estimates of the groups of vervet monkeys on Timothy Hill, St. Kitts in 1972 (McGuire 1974) and in 1982 (Fedigan unpublished).

	Timothy Hill I (1972)	Timothy Hill I (1982)
Adult Male	3	17
Subadult Male	-	2-3
Adult Female	3	21
Subadult Female	2	2
Juvenile	2	6-7
Infant	3	6
Unidentified	0	4
Total	16	54-60

	Timothy Hill II (1972)	Timothy Hill II (1982)
Adult Male	2	10-11
Subadult Male	-	4-5
Adult Female	3	19
Subadult Female	0	3
Juvenile	3	13-16
Infant	6	9
Unidentified	0	0
Total	14	58-63

	Timothy Hill III (1972)	Timothy Hill III (1982)*
Adult Male	2	9-10
Subadult Male	-	2-3
Adult Female	4	18
Subadult Female	0	2-3
Juvenile	2	8-7
Infant	7	11
Unidentified	0	0
Total	15	50-53

All 1972 figures were after fission (see McGuire 1974).
* Group observed in this study.

americana, and a variety of shrub and grass species. The drainage ravines of the hill support large trees, such as Bursera simoruba, Piscardis piscidula and Hippomane mancinella, which grow to a maximum height of 12 meters. At the base of Sir Timothy Hill there is a flat area which supports dense stands of sea grape (Coccoloba uvifera) along the other shores, a large pasture area, a mancineel grove (Hippomane manicinella) and an extensive mangrove thicket (Rhizophora mangle) which surrounds a small saline lake. Throughout this flat area there are intermittent stands of clammy cherry trees (Cordia obliqua) and coconut palms (Cocos nucifera).

The area is unusually dry in comparison to the remainder of the island. Daily rainfall levels were collected by the National Agriculture Corporation (NACO) at a site about one mile from the study area. Over the 8 month period of this study 46.1 cm. of rain fell at this location, the monthly levels varied from 1.7 cm. to 15.3 cm. The temperature of St. Kitts ranges from 18° C to 32° C. The low level of rain fall, the high temperature and the low water retension ability of the soil, were all factors contributing to the xerophytic nature of the study area.

B. Behavioural Sampling

Free ranging St. Kitts vervets are difficult to observe, and the data collection procedure utilized here reflects this. A focal animal sampling technique was employed in order to obtain the most complete record possible of not only the focal animals behaviour, but also to obtain a record of those behaviours directed to the subject by others (Altmann, 1974). The length of the test session was 5 minutes. This short focal animal length was necessary in order to get an adequate number of focal animal samples in areas where the subject could easily be lost by the observer, such as in the very dense sea grape/acacia habitats.

During each focal animal sample, the frequency and the duration of the behaviours exhibited by the subject and those directed to it were recorded on data sheets. The time of each change in state was recorded using a standard

hand held stopwatch. Those behavioural categories which were used in this study are listed in Appendix 1. The behaviours sampled were selected for their potential ease of observation under the field conditions, as well as their potential to be influenced by ecological variables.

Ideally, the selection of the individual focal animal subject is made by randomly selecting individuals from the population throughout one complete rotation. Unfortunately, not all of the animals in the population could be recognized individually. Thus, when initiating a series of focal animal sessions on the group, the first animal seen was normally selected as the focal subject. Thereafter, the subject was selected from a different age/sex group. An attempt was made to select a focal animal from all age/sex categories before an animal from the first age/sex category was selected a second time. If possible, a continuous record of a subject's behaviour was recorded for 10 minutes and this was considered equivalent to two five minute sessions. It was frequently not possible to maintain continuous visual contact with a subject for as long as 10 minutes, especially when the animals were moving through densely vegetated areas.

As well as recording strictly behavioural information, the focal animal's location within the group's home range was noted using an X,Y coordinate system. This allowed the behaviours recorded to be related to the ecological conditions of the areas in which they were expressed. Also, at the beginning of each focal animal session, the age/sex composition of the group was recorded.

The categorization of age/sex groups was based upon observations of those physical attributes of the animals which were most apparent. Adult males were large with well developed musculature and their scrotum was easily visable. Subadult males were intermediate in size between fully adult individuals and juveniles, their scrotum was commonly visable but it was not as large as that of an adult male, and their shoulder musculature was not as well developed as an adult male's. Adult females were smaller than adult males with not nearly as well developed musculature, also their elongated nipples were easily seen,

even from a distance. Subadult females were the most difficult group to identify and were commonly defined by the lack of traits characteristic of other age/sex groups. They lacked elongated nipples, but only rarely was it possible to see their small nipples. Their intermediate size, between that of an adult and a juvenile was a useful characteristic to identify them. Juveniles could be easily identified on the basis of overall body size and shape. Since the scrotum of the male juveniles and the nipples of the female juveniles were poorly developed and extremely difficult to see, no attempt was made to distinguish between the sexes. Infants were easily identified on the basis of size. An animal was considered an infant from the time of birth until the time of birth of the next year's infant cohort, whereupon they were subsequently considered juveniles. The field appraisal of age/sex classes were checked against captive animals on St. Kitts of known age and sex and this estimate proved reliable.

In order to be able to give detailed information on the foraging behaviour of these animals, whenever an animal was observed feeding, the species of plant and the part of the plant being fed upon, were both noted. With small shrubs and annuals it was often not possible to tell what part was being utilized.

C. Ecological Sampling

To meet the objectives of this study it was necessary to formulate an experimental design which would sample the ecology of the areas used by the monkeys, without making assumptions about which characteristics were important to the monkeys. It would have been invalid to discuss the behaviours exhibited by the focal animals in subjectively defined habitats. These arbitrarily defined categories would not necessarily be meaningful categories to the monkeys. In order to avoid this, a grid system of 100m. by 100m. quadrats was placed across the entire home range of the group. Comparisons could then be made between quadrats which were not subjectively defined by the researcher. In fact the quadrats often contained a number of what would have intuitively been considered quite different habitats.

The group of vervets commonly used about 51 of these quadrats. The large number of quadrats which were utilized made it impractible to sample the desired ecological variables in each quadrat, in detail. To assess the ecological characteristics of the quadrats a system of 10m. by 10m. plots were randomly placed in each of nine distinct types of habitats. The habitats examined were: pasture, mangrove swamp, seagrape/acacia on the Atlantic coastline, seagrape/acacia on the Caribbean coastline, tall treed drainage ravines, cactus dominated slope, grass dominated slope, shrub dominated slope and tall treed plateau. The plots were intensively examined so as to determine their score on each of the ecological variables (Table 2). The values of the ecological samples obtained from the plots were considered to be representative of the habitat as a whole. The proportion of each of these distinct habitat types in each quadrat was then calculated. Finally, the level of each ecological variable for the quadrat was calculated by summing the proportion of the each habitat type in a quadrat, multiplied by the habitat's value on a particular ecological variable. This resulted in each quadrat having its own independent value for each of the ecological variables examined.

A considerable body of literature exists on the methodology of designing a plot sampling system (see Gysel and Lyon, 1980). The fine grained level of sampling that was desired for this study limited the number of plots that it was feasible to sample, to one per habitat type. The positioning of the plot within the habitat type was done randomly. It was decided to use a 10m by 10m plot because it was felt that this size would give an accurate representation of the plant diversity in each habitat. Nine study plots were set up across the group's home range, one in each of the habitat types. The plots were sampled only once, at about midway through the study. It was not possible to sample the plots more than once during the course of the field work since it took between 2 to 3 days to sample each plot.

A measure for each of 20 ecological variables was determined for each plot (Table 2). Initially, samples of each of the plant species represented in the plot were collected in order to be able to positively identify each species

TABLE 2 : ECOLOGICAL VARIABLES EXAMINED
(density and diversity indices represented in three size classes)

Plant Density	low	(0.0m - 0.5m)
	med	(0.5m - 2.0m)
	high	(>2.0m)
Food Plant Density	low	(0.0m - 0.5m)
	med	(0.5m - 2.0m)
	high	(>2.0m)
Plant Diversity	low	(0.0m - 0.5m)
	med	(0.5m - 2.0m)
	high	(>2.0m)
Food Plant Diversity	low	(0.0m - 0.5m)
	med	(0.5m - 2.0m)
	high	(>2.0m)
Cover		
Structural Complexity (1-4)		
%Area Covered by Plants		
%Area Covered by Food Plants		
Human Disturbance (1-5)		
Mean Canopy Height		
Maximum Canopy Height		
Amount of Open Ground%		

accurately by keying them at a later date. In order to be able to determine the density of each of the species found in the plot, the number of individuals of each species were counted. For very small and abundant species such as the grasses, or some of the small succulents, a 1 m^2 sub-plot was set up, and the number of individuals in the sub-plot was determined, from which the total number of individuals present in the plot was extrapolated. In all cases, the number of stalks was considered to be the number of individuals. The plant density value for the plot was calculated as the sum of number of individuals of each species in the plot divided by the area of the plot. Thus, the units of measure for density was the number of individuals per square meter. It was felt that in the discussion of plant density it was undesirable to treat all plants equally, independent of size. The density of three separate size classes of plants were analysed independently. The size classes were; 0m. to 0.5m., 0.5m. to 2m., and greater than 2m. If these size class distinctions were not made, the small abundant plants would have contributed disproportionately to the density value obtained in all plots. At the end of the field season, the density of all of the plant species on which the vervets were observed to feed was calculated, and a level of food plant density was determined.

To determine the effect of the diversity of the available plant and food plant species on vervets' behaviour, diversity was determined by relating the total number of each species to the total number of individuals. To allow comparisons to be made to other studies, the commonly used Shannon-Wiener index of diversity was used. This function is defined as;

$$H' = -\sum pi(\log pi)$$

where pi is the proportion of the samples belonging to the i th species (Krebs, 1978b). This index most adequately represents the two aspects of diversity; the number of species, and the number of plants (Harvey, 1977; Clutton-Brock, 1977b). As with density, the plant diversity and food plant diversity variables were estimated using the three size classes of plants.

An attempt was made to determine the ability of each quadrat to provide the vervets with cover. Typically the level of cover has been assigned

by ranking habitats in a qualitative manner, based upon the ease of visibility of the monkeys (Fairbanks and Bird, 1978; Kummer, 1968). This method is somewhat biased because it is seldom known to what extent an area can completely conceal an animal.

For this study a measure of cover was obtained by estimating how much of a 10 meter pole could be seen by an observer viewing from a 10 meters distance, while seated on the ground. The rationale behind this method is that it would estimate the ease of viewing at all levels of the canopy. The choice of a 10 meter high pole was based upon the finding that the canopy was rarely taller than this height. In order to standardize the sampling of the cover in each habitat, 16 estimates were taken in each plot and the values were averaged.

In each plot the mean and maximum height of the plants was determined. Mean canopy height was estimated by averaging the height of all plants, except those plants that belonged to species that are very small and abundant such as grasses and ground level succulents. Maximum canopy height was simply the height of the tallest individual plant.

The percentage area covered by all plant species, and subsequently the area covered by all food plant species was determined for each plot. This index was obtained by summing for all individuals, the area of the ground that each covered. It was possible to get values for this index that were greater than 100% in habitats that had two or more layers. While determining the area covered by all plants it was possible to determine the amount of ground that was not covered by any plant individuals, thus a value for the amount of open ground was obtained.

Finally, for each plot two qualitative ranked measurements were made. The first was an estimate of how intense the level of human disturbance was in the area. Human disturbances were either in the form of direct use, such as walk through areas, or they were disturbances such as altering the environment of an area by cutting trees for fire wood or by grazing sheep. The second qualitative measure was of the structural complexity of an area. Open pastures receive the lowest rank, while areas with tall trees and dense understories

receive the highest rank.

One objective of the study was to determine the amount of time the vervets spent in various parts of their home range. Since it was impossible to sample the quadrats equally at all times of the day, it was not possible to use the number of focal animal sessions in a quadrat as the measure of proportional time use. So in order to determine the proportion of time the group spent in each area, twelve transects were placed throughout the study group's home range in such a manner that at least one transect was in each of the habitat types. The number of vervets counted along a transect was considered a true census of the area through which the transect passed. In order to calculate the population density for an area, it was necessary to determine the actual area that was being surveyed on each transect. To do this, the perpendicular distance to the transect midline for each individual, was used to estimated and the average was considered one half the transect width. For some transects, where the width of the transect was actually known, such as those passing through clearings which were ringed with dense vegetation, the actual width was used. The population density estimates of the transects were made by dividing the total number of animals seen on a transect during all tests by the area of the transect and by the number of times that transect was walked.

$$P = No / (WxLxN)$$

Where:

P=population

No=Total number seen

W=width of transect

L=length of transect

N=number of times the transect was walked

Multiplying the denominator by the number of times the transect was walked compensated for unequal sample sizes. To ensure that each time a transect was

walked, it was independent of the preceeding time, the same transect was never walked twice within a 30 minute period. Normally the same transect was not walked more than twice a day. To examine how habitat use varied throughout the day, the time at which the transect was walked was recorded. To examine diurnal variation in habitat use, subpopulations were selected from the population estimates over the entire day, based upon the time of day. For the purpose of this analysis, the day light hours were divided into four periods; dawn to 9 A.M., 9 A.M. to 12 noon, 12 noon to 3 P.M., and 3 P.M. till dusk. Every transect was walked at least 10 times in every daylight hour, to obtain a sufficiently large sample to compare habitat use at different times of the day. Since the area of each transect was known, it was possible to assess the ecological characteristics of the transects by extrapolation from the 10m by 10m sample plots, as was done for the quadrats in the grid system.

III. GENERAL DESCRIPTION OF THE ECOLOGY OF THE STUDY GROUP

Despite the sharp increase in the number of primate ecology studies that have appeared in the literature, most of what is known about Cercopithecus aethiops has come from field studies that were either of relatively short duration or qualitative in nature. The aim of this chapter is to describe the feeding and ranging behaviour of the study group, primarily to provide a general understanding of the conditions experienced by the group, and to compare the results obtained from this study with those from other studies on this species.

A. Ranging Behaviour

Throughout this study daily records were kept of the study group's movements through the various parts of its home range. This was done in two fashions; firstly by dividing the home range into 100m. by 100m. quadrats and tabulating the number of hours observed in each quadrat, and secondly, by utilizing the transect system to sample the locations of the group members in an systematic fashion. The study group's home range consisted of 51 of these 100m. by 100m. quadrats. The frequency of use varied significantly between quadrats. The group spent 75% of their time in only six quadrats. These results are directly comparable to Struhsaker's (1967a) observation, for he employed the same system to record his group's ranging behaviour, utilizing the same sized quadrats. He found that one group of East African vervets spent 75% of their time in 8 quadrats while the other spent 75% of their time in 20 quadrats. Since the frequency with which each quadrat was sampled in this study was not equal, the frequency of use of a quadrat cannot be adequately determined. So the time spent in each quadrat is not employed in later analyses to indicate relative use. However, the transects were sampled equally, and thus are free of this sampling problem. The transect data is a more reliable estimate of home range use because it samples all areas equally. Throughout the duration of the study 57% of the animals seen in all transects were found in only three of the twelve transects. These three transects represent only 25% of the area sampled. There was little monthly variation in this value (from 55% to 61%). The analyses

of the use of quadrats and transects demonstrates that the group spent the majority of its time in a fairly restricted area, suggesting that the vervets of the study group were selecting the areas which they were using. The degree to which this selection is related to specific ecological conditions is discussed below.

The vervets of this study group were very dispersed. It was not uncommon to find individuals of the group spread from one end of their home range to the other. This distance is just under a kilometer. There did appear to be a relatively cohesive "core" group, containing the majority of the adult and subadult females, their associated infants and juveniles and a couple of adult and subadult males. It was the remaining adult males of the study group which seemed to be scattered over the greatest area. Solitary animal sightings represented 23% of the sightings in the transects in which any animal was seen, half of these were adult males. This differed significantly from what would have been expected if all adults and subadults of both sexes had an equal chance of being solitary (X^2 = 5.4, $P<0.05$, d.f.=3).

The level of dispersion that is reported in other studies of vervets is highly variable. Struhsaker (1967a) and Cheney (1981) report that the vervets of Amboseli form relatively cohesive groups. Dunbar (1974) expresses the same opinion of the vervet group he studied in Senegal. The vervet groups that were observed on Lolui Island, Lake Victoria were occasionally up to 200m apart (Hall and Gartlan 1965), while the vervets at Chobi were dispersed up to 500m (Gartlan and Brain, 1968).

It is commonly reported that group dispersion increases as a function of low food abundance (Gartlan and Brain, 1968; Eisenberg et al., 1972; Moreno-Black and Maples, 1977). Although food abundance data were not collected to provide seasonal values, no impression was received that dispersion increased in the study group in the dry season when food resources decreased. Also when fruit was in extremely high abundance, no decrease in dispersion was noted. The increasing population of vervets in the area (Fedigan unpublished) would suggest that the group was not short of food. Taken together, the

evidence would not lend support to the purported relationship between high levels of dispersion and low levels of food resources.

The mean daily distance travelled in one day by the study group was 2.4km. This distance is comparable to other reported groups. Struhsaker (1967) describes how two vervet groups in the Amboseli Game Reserve moved on the average 1.18 km daily. Kavanagh (1981) reports average daily ranges of 2.27 km. and 0.94 km. for two groups of vervets. Brain (1965) describes a vervet group which moved 11 miles in 24 hours.

The group size of 50 animals for this group is within the range of those reported elsewhere, though it is at the upper end of those reported. In East Africa Struhsaker (1967a) observed group sizes ranging from 7 to 53 animals, with a mean of 28. Lancaster's (1971) study group contained 55 animals, and Gartlan and Brain (1967) reported that the typical group size on Lolui Island, Lake Victoria was 11 animals. In West Africa, Galat and Galat-Luong's (1976) study group contained 42 animals and the average size of the groups studied by Kavanagh (1981) was 31 animals. On St Kitts, McGuire (1974) reported groups sizes ranging from 4 to 65 animals.

The home range size of the study group was 0.54km^2. Home range was defined as the area which any group member used over the period of study. Because of the differential use of areas and the dispersed nature of the group, a large proportion of this area was used rarely and only by a small number of animals. In Amboseli, Struhsaker (1967a) found that the average home range size for four groups was 0.414km^2. Kavanagh (1981) describes the average home range size for all of the West African vervet groups he studied as 0.46km^2. McGuire (1974) reported the home range sizes of the groups of vervet monkeys he observed on St. Kitts as having home ranges from 0.16 km^2 to .44km^2.

When comparing the population densities of vervets from the studies made in East and West Africa to those of St. Kitts, a large amount of variation is evident. The population density of the vervet group examined in this study was 90.0 individuals per km^2. This was calculated simply by dividing the

known group size by the group's home range size. In East Africa, Struhsaker (1967a) found a lower average density of 58 individuals per km². The West African studies of the vervet report strikingly different population densities. Kavanagh (1981) presented the population densities of four groups, which ranged from 18 to 149 individuals per km², with an average of 98 individuals per km². Galat and Galat-Luong (1976) found an extrordinarily high population density of 239 individuals per km² in Senegal. The population density of the study group is well within the limits reported for other groups.

Using the home range sizes, group sizes and population densities of the vervet populations reported in the literature, and discussed here, it was found that there is no simple correlation between the home range sizes and the population densities of vervets ($r=-0.1842$, $P=0.318$, $d.f.=11$), however, there is a trend for home range size to increase with group size ($r=0.5370$, $P=0.068$, $d.f.=11$).

B. Sleeping Site

All animals came together at night at a steep drainage ravine. This ravine contained some of the largest trees in the study site. The sleeping site was located almost 800m from the areas most intensively used throughout the day. Animals started arriving in the sleeping site as early as 4 p.m. and continued arriving until dark. The majority of the animals would arrive just before dusk. One of the transects passed directly through the sleeping site. By far the majority (94%) of the trials of this transect in which there was some animal sighted, occurred after 4 p.m. The largest number of animals seen on this transect occurred at 6:30 p.m., just before sunset.

The selection of this location as the group's sleeping site may have served to protect the vervets from predation. It was difficult to get to this area because it was removed from frequently travelled routes, and it was directly above the ocean, which prevented approach from that direction. Despite the very protected nature of the sleeping location, the selection of this site is not totally clear because the major predators of monkeys on St. Kitts are wild

dogs and human hunters, neither of which are nocturnal hunters. In fact on St. Kitts there are no predators which hunt at night. The arguement that the selection of a sleeping site was made in order to decrease the risk of predation is further weakened by the fact that the vervets used the same location every night. With repeated use of one area there is an increased probability that a predator will learn of its location and continually prey upon the group. Struhsaker (1967a) and Galat and Galat-Luong (1977) describe vervets selecting different sleeping sites on different occasions.

Monkeys were repeatedly observed in the same trees at dusk, presumably they remained in those trees throughout the night. It was not possible to test this, since individuals frequently started moving before it was light enough to identify them. There was no evidence that the monkeys split up into sleeping subgroups which were spatially isolated, as has been described by Struhsaker (1967) for the East African vervet. All sleeping trees were within 50 meters of each other.

C. Daily Pattern

To describe quantitatively the daily pattern of the group, an activity budget of the group's daytime activity was calculated. This was done by tabulating the amount of time the average individual spent engaged in each of five behaviours, for each hour sampled. The distribution of the time spent engaged in the five most frequently observed behaviours is represented in Figures 1 through 5. From the activity budget the average day plan was determined.

After the group left the sleeping site it travelled rapidly down the hill into the flat bay area. Typically, this progression involved some foraging but little social behaviour. During this time, it was not uncommon for the five minute focal animal sessions to be composed of only locomoting and resting. In approximately 30 minutes the group would cover up to 700 meters. It was during this time that the group started to disperse. There would commonly be a 30 minute temporal separation from the time the first group members entered

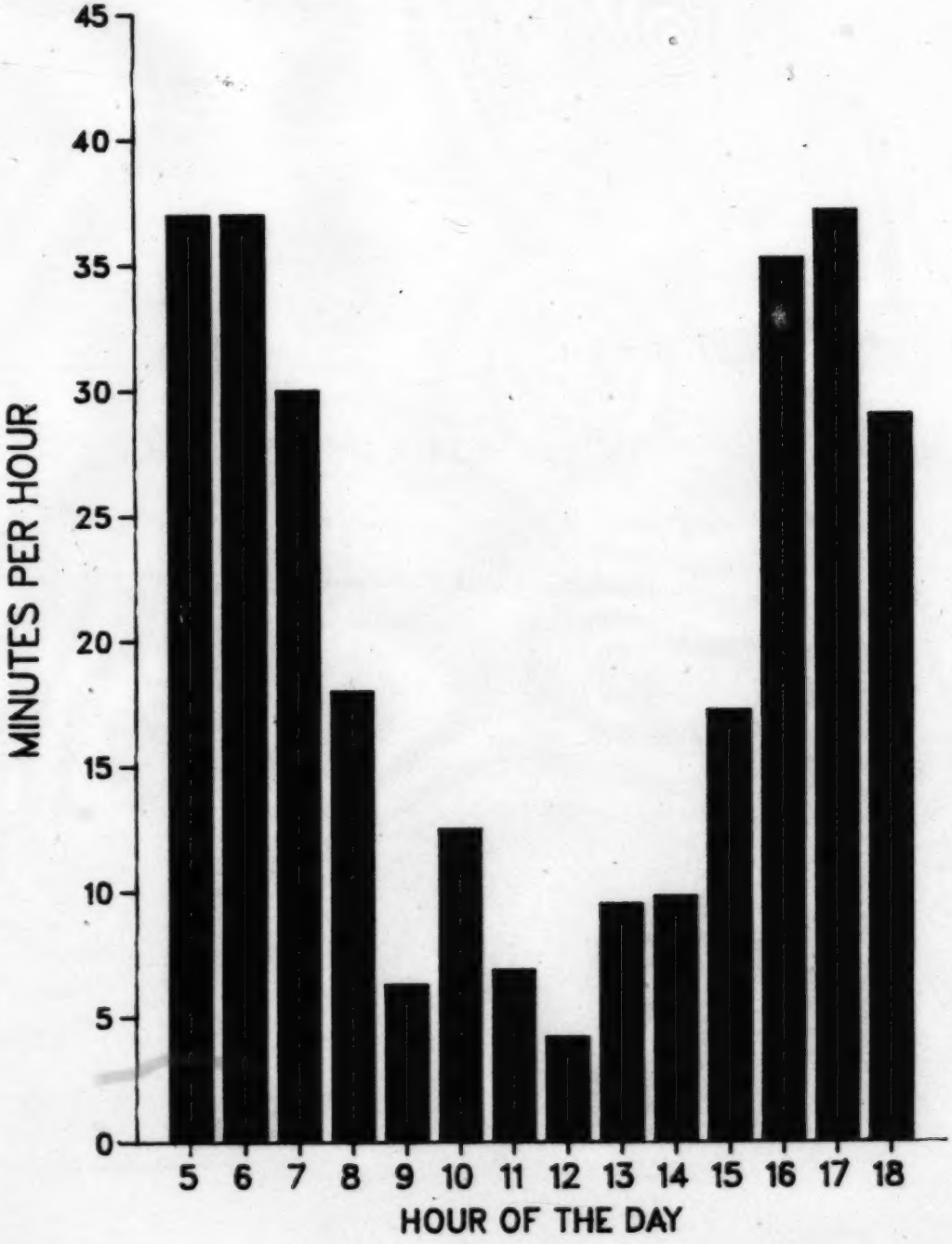


Figure 1: The diurnal distribution of the average number of minutes per hour that any individual vervet monkey in the St. Kitts study group was observed to be feeding.

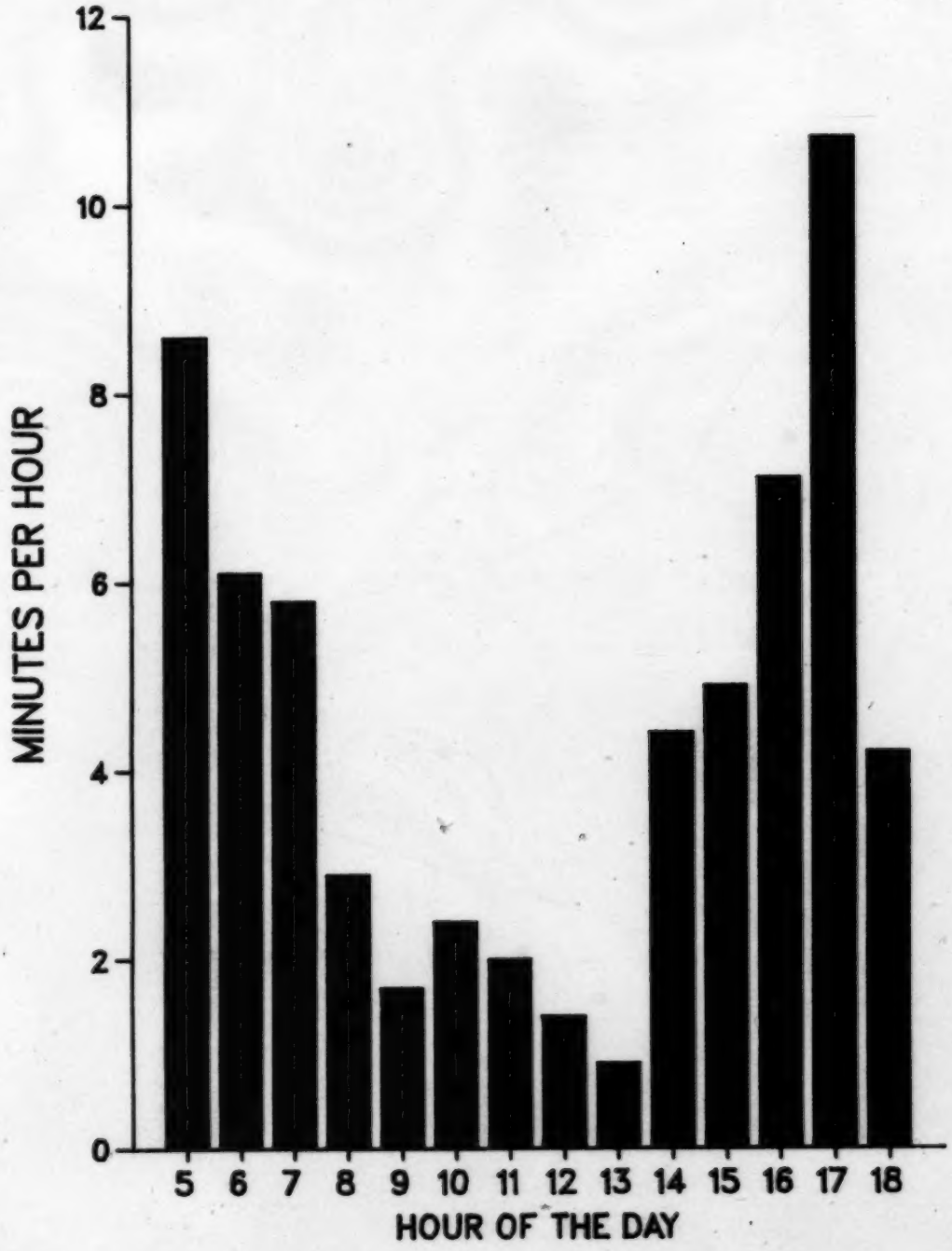


Figure 2: The diurnal distribution of the average number of minutes per hour that any individual vervet monkey in the St. Kitts study group was observed to be locomoting.

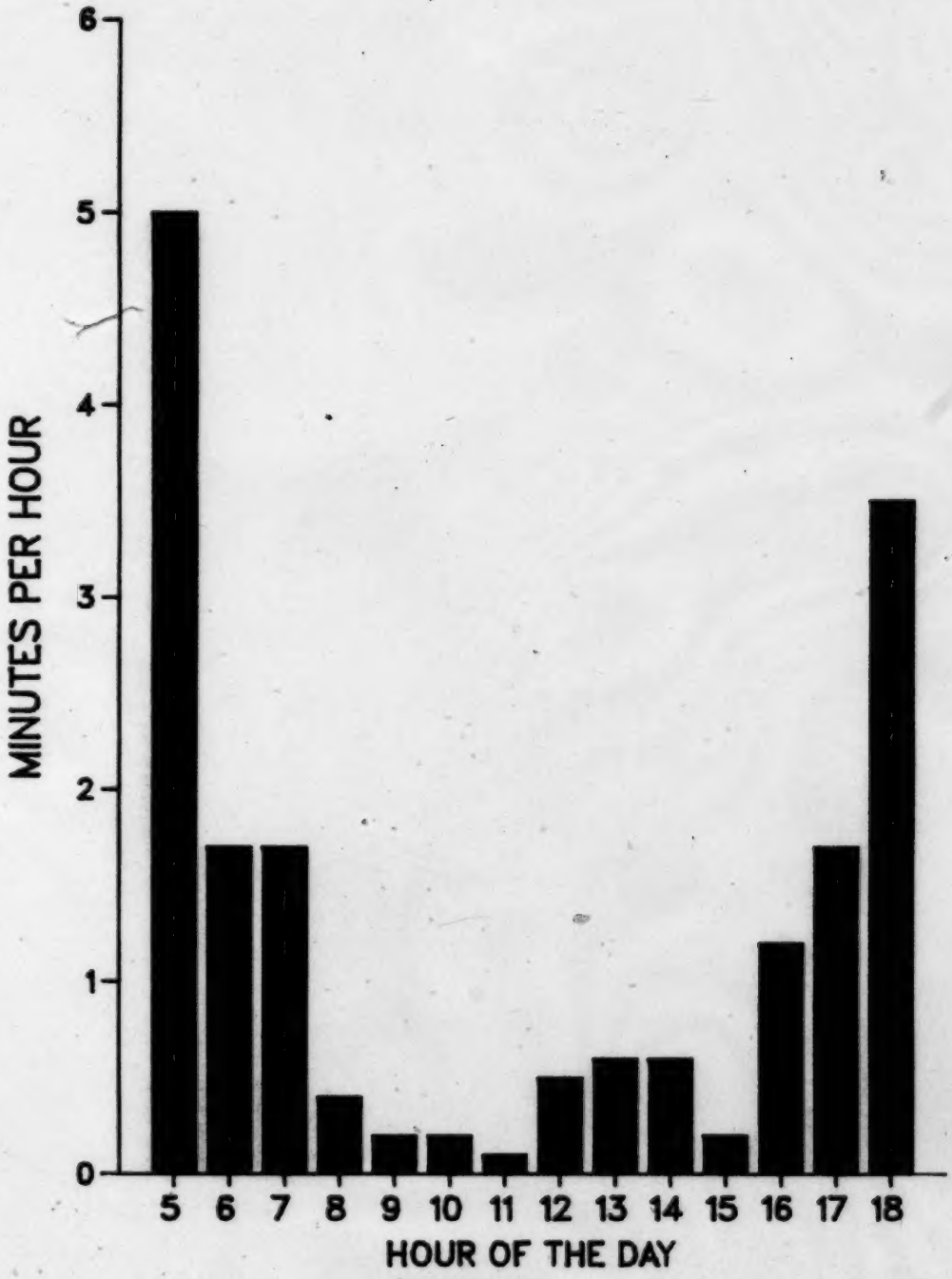


Figure 3: The diurnal distribution of the average number of minutes per hour that any individual vervet monkey in the St. Kitts study group was observed to be playing.

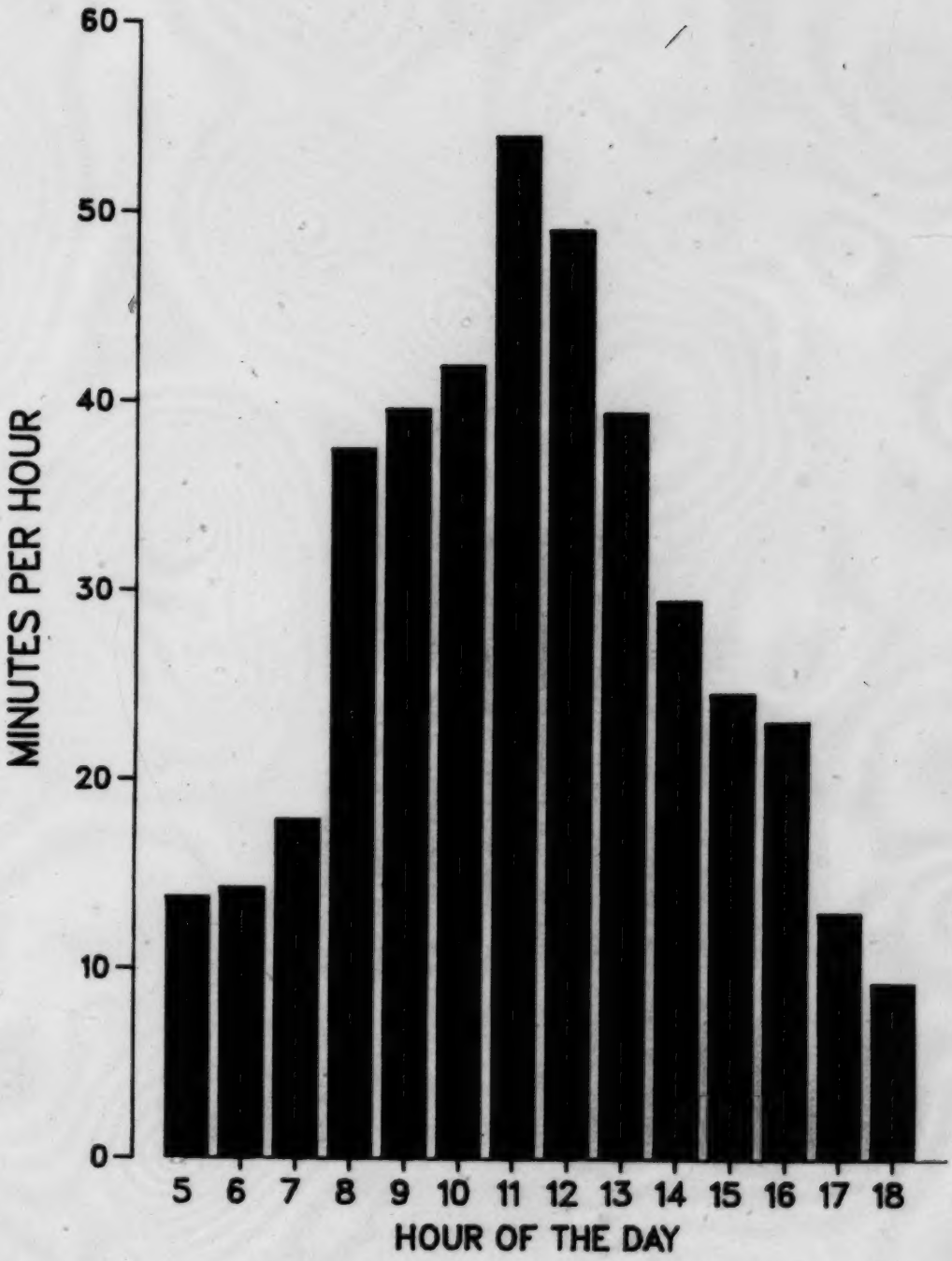


Figure 4: The diurnal distribution of the average number of minutes per hour that any individual vervet monkey in the St. Kitts study group was observed to be resting.

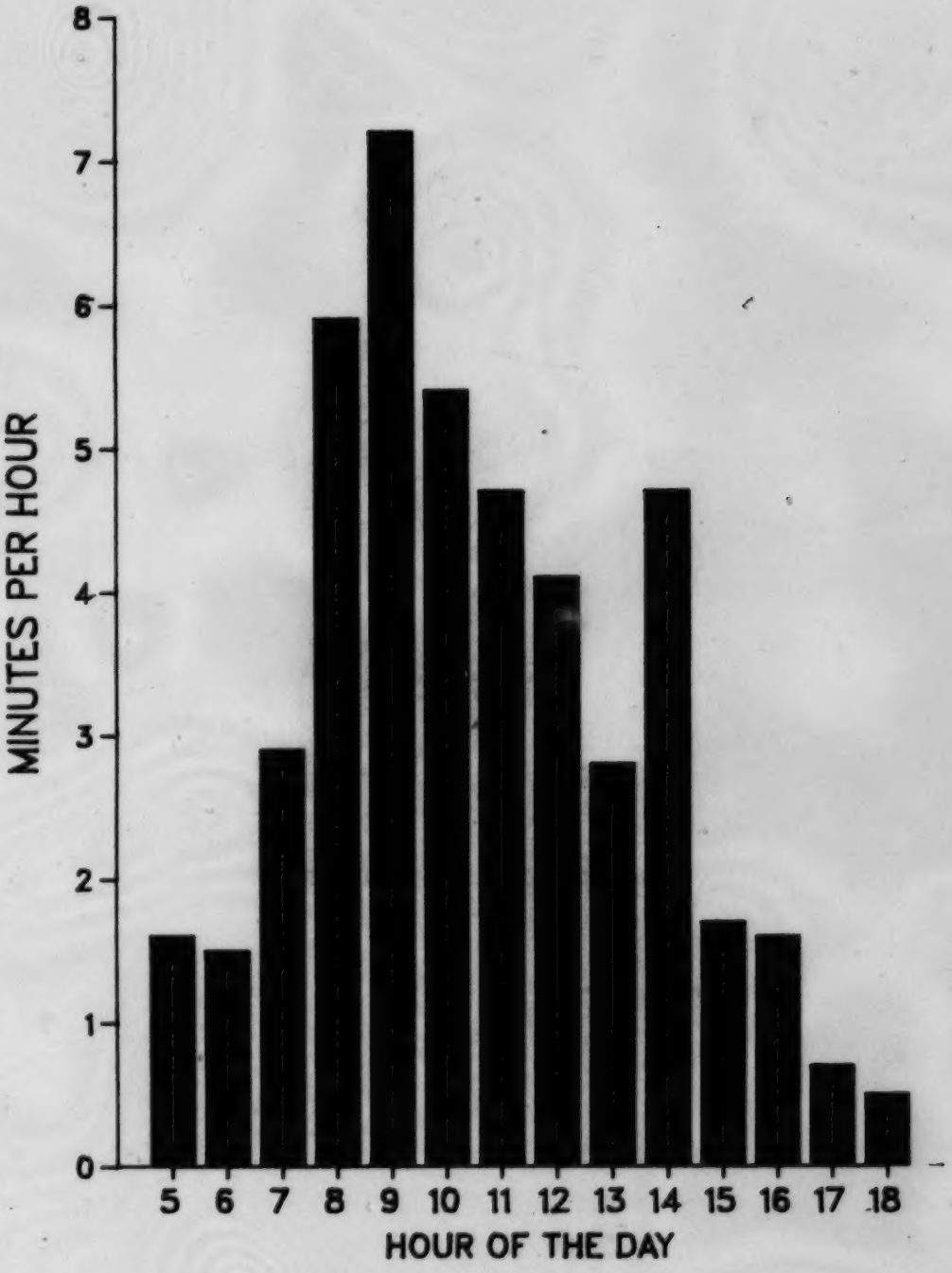


Figure 5: The diurnal distribution of the average number of minutes per hour that any individual vervet monkey in the St. Kitts study group was observed to be grooming.

the bay area to the time the last animal entered. This temporal separation would represent a spatial separation of over 400 meters. Once in the bay area, animals foraged for a 2 to 3 hour period, during which time they would move from one side of the bay to the other. After this foraging period, animals would seek out areas of shade and spend the next 7 to 8 hours socializing and resting. There would often be foraging bouts of short duration, dispersed throughout this resting period and some movements, of less than 100 meters, occurred in the direction of the sleeping site. Between 3 and 4 pm. the animals became more active and started foraging as they slowly made their way towards the sleeping site. During this late afternoon period, there were often extended bouts of play. By 6:30 pm. the majority of the individuals had made their way back to the sleeping site where they foraged and socialized until sunset. There was very little seasonal variation in this pattern of range use. However, the animals did respond to local abundances of food sources by increasing their foraging time in those areas.

The members of the group spent the greatest percentage of the sampled time resting. They rested for 54% of the total daylight hours. This would imply that for the majority of the day the vervets were selecting habitats in which they can rest. The vervets spent 28.2% of their day feeding. Feeding was unevenly distributed throughout the day, the majority of it was done in the early morning and late afternoon. The first and last three hours of the vervets' active day included 71% of their feeding time. Throughout the whole day the vervets only spent 8.5% of their time locomoting, this entails just over one hour of actual time. In this short time they were able to cross their entire home range length and then return to their sleeping site, covering a distance of over 2km. In one day the average vervet would spend about 45 minutes being groomed or grooming others. This entailed about 6.1% of total time sampled. Considering the fact that certain age/sex classes do little grooming, specific animals are undoubtedly engaging in grooming for much longer periods. Similarly, during the day the average amount of time spent engaged in play was 17.6 minutes which is aproximately 2.6% of their day, but since adults rarely engaged

in play, the juveniles and infants were contributing most of this time.

It is interesting to note that high frequencies of play accompanied high frequencies of foraging and play did not peak at similar times to either grooming or resting behaviours. The juveniles and infants were commonly observed to play while most members of the group were foraging and travelling.

D. Feeding Ecology

Vervets have been described as "opportunistic omnivores" (Struhsaker, 1967). This categorization would seem to accurately describe the foraging pattern employed by the members of the study group. The vervets fed on some part of most of the common plant species available to them. Of the 71 plant species that were identified from the plots, they were observed feeding on 28. Of the remaining 43 plant species, 20 had a density that was lower than 1 per 100 m^2 in the habitats in which they were found. The vervets were observed feeding on clammy cherry fruit (Cordia obliqua) most frequently (Table 3). Different individual clammy cherry trees bore fruit in seven out of the eight months of the study. Clammy cherry trees were also important to the vervets as a source of shade and cover.

Acacia farnesiana, commonly called acacia, had the second highest frequency of observed feedings. Acacia provided some form of food throughout the entire study period. The vervets were observed to feed on the pods, beans, bark, leaves and flowers of acacia. Gumbo Limbo tree (Bursera simaruba) was the next most commonly eaten food plant species, but it was only important during the first two months of the study and it was abandoned when its fruit were no longer as abundant. After these first three sources there is a marked decrease in the number of observed feeding bouts of any one species. A variety of trees contribute approximately equally to the vervets' diet. The group was frequently observed feeding on the food category of small unidentified plants. This category was composed of annuals and shrubs which were abundant in disturbed areas and characterised the initial stages of

Table 3: The composition of the diet of the vervet monkey (*Cercopithecus aethiops*) study group. (Based on observed frequency of feeding).

Food Plant	Number	Percentage
Clammy cherry (*Cordia obliqua*)	594	34.2
Acacia (*Acacia farnesiana*)	235	13.5
Unidentified shrub or grass	239	13.8
Gumbo limbo (*Bursera simurba*)	111	6.4
Insects	101	5.8
Unidentified tree	92	5.3
Grass	91	5.2
Limp tree (*Croton balsamifera*)	70	4.0
Pasture Tree	64	3.7
Remaining food plants	140	8.1

secondary growth.

Information was recorded on the proportion of the various food parts in the study group's diet (Table 4). Fruits were the plant part that was most commonly eaten, accounting for 34% of the total. The food species upon which the greatest amount of time was spent foraging was "clammy cherry trees" and except for occasionally eating leaves from this tree, it was only exploited for its fruit. Pods accounted for 12.2% of the plant parts eaten, the only species from which pods were eaten was Acacia farnesiana . This demonstrates the importance of this food species. There was little seasonal variation in the importance of the various food parts. There was never a change in ranked importance of any of the top five most frequently eaten food parts.

The vervets were never observed feeding on any vertebrate species. Meat eating has been reported from a number of different studies of vervets. Galat and Galat-Luong (1977) reported that the Senegal vervet population they studied preyed upon both birds and Nile rats (Arvicanthus nicotus). Predation on birds eggs has been reported in East African vervets (Struhsaker, 1967a), St. Kitts (McGuire, 1974) and in South Africa (Skinner and Skinner, 1974). While there were birds nesting in areas commonly used by the vervet group of this study, no predation attempts on eggs or young were observed.

Although fiddler crabs (Uca sp.) and hermit crabs (Pagurus sp.) were both very abundant in the area, no member of the study group was ever observed feeding on them. In Senegal, Galat and Galat-Luong (1977) report that 52% of the time spent feeding was involved in hunting fiddler crabs (Uca tangeri) which comprised a major item in the vervets' diet.

Members of the study group were commonly observed turning over sticks, rocks and dung, presumably in an attempt to forage for a variety of beetle species. They also were commonly observed leaping at grasshoppers and catching them by hand. Feeding on insect species made up only 5.8% of the total observed feeding bouts. This level of insect foraging is considerably less than that reported elsewhere for the species. Galat and Galat-Luong (1977) reported that 26% of the vervets' diet in Senegal was composed of animal

Table 4: The frequency of use of the available plant parts by the vervet monkey (*Cercopithecus aethiops*) study group, St. Kitts.

PART	NUMBER	PERCENTAGE
Fruit	616	34.2
Seeds	250	13.9
Pods	218	12.1
Flowers	86	5.0
Insects	77	4.3
Leaves	48	2.7
Roots	23	1.3
Buds	11	0.6
Bark	9	0.5
Unknown	389	21.6

foods. Kavanagh (1978a) reported that Buffle Noir the animals spent 28.7% of their time eating insects.

In this study, there seemed to be a distinct age/sex difference in the observed rate of foraging on insects. Adult females were observed feeding on insects 22% more frequently than any other age/sex class.

Precise information was collected on the phenological cycling of the 11 most important food plant species. Weekly reports of the fruiting or flowering stages of these species were kept, as well as comments on the relative availability of leaves. It was clear that the phenological cycle of the food species was a major factor influencing the diet of the vervets. For example, when the clammy cherry trees did not bear fruit, the vervets rapidly started foraging on a number of plant species (7) on which they had never before been observed to feed. Another clear example concerns seagrape (Coccoloba uvifera). The fruit of this species was only abundant for the month of October, at which time it featured predominately in the group's diet. In the months when the fruit of the seagrape was present but not abundant, seagrape was largely ignored. The opposite trend was also evident. Some food items were abundant over the whole study period but were only utilized for a small proportion of the total time they were available. The time when these food species were utilized corresponded with a lack of more desirable food plants.

Since the length of the study was only eight months, and thus observations were not made throughout the whole annual cycle, data upon the effect of seasonality is incomplete. However, the study period was such that it included both the driest and wettest periods of the year. The seasonal variation in exploitation of food species noted in this study did not appear as marked as has been described elsewhere (Kavanagh, 1978a), possibly because the differences between the wet and dry season on St. Kitts are not acute. The percentage of the sampled time which this group spent feeding is comparable to Kavanagh's (1978a). He found that at Buffle Noir the vervets spent 24.5% of the sampled time feeding and at Kalamaloue they spent 20.0% of their time feeding. The St. Kitts study group spent 28.2% of the sampled time feeding.

The foraging data clearly indicates a preference for specific food types, and there is a wide variety of potential food sources (eg. crabs) which were not exploited. Certain plant species were not exploited by the study group, but other studies of vervets elsewhere found the group members utilizing these same species. For example, this study group did not forage on mangrove (Rhizophora mangle), yet Galat and Galat-Luong (1976) reported the exploitation of mangrove species in Africa. Indeed, the vervets in the present study and those of the Galat and Galat-Luong's study show quite different dietary tastes. The St. Kitts vervets ignore the abundant and readily available crabs and mangrove food resources, whereas the West African vervets exploited them as a major resources.

Wrangham (1981) observed intense competition for water in groups of vervet monkeys in the Amboseli National Park, Kenya during periods of water shortages. Wrangham states that the observations he made imply that the water stress was so severe on some individuals that they were unable to maintain adequate physical condition. McGuire (1974) suggested that the availability of water might be limiting the vervet monkeys living on the dry peninsula of St. Kitts. While there were prolonged periods when the study group did not have access to standing water, there was no obvious evidence that the study groups were water stressed. A number of the fruits that were a major part of the study group's diet were very succulent and may have in themselves provided an adequate supply of water. At periods of time when there were only a couple of areas which contained standing water, the vervets did not appear to associate in these areas more than when the water was not available. Also, no direct conflict was observed over access to the standing water. This evidence would suggest that the vervets of the study group were not limited by their access to water, and also that they were not selecting areas, based upon the availability of standing water.

The objective of the previous discussion was to provide some generalizations about the ecology of the the area of the study group. However, of equal importance are the differences in ecology that exist within one group's

home range. The following discussion will first analyse this variation and then state how the vervets responded to it.

E. Interrelationships Between the Ecological Variables

The vervets in the study group had a variety of habitats available to them within their home range. The level for each of the ecological variables previously discussed was determined for each habitat type using the plot system of sampling. This resulted in the level of 20 ecological variables being calculated for each of the 44 quadrats where focal animal data were collected. Using this number of values for further analysis would have been extremely lengthy and difficult to conceptualize. Thus, a factor analysis was carried out to simplify the analysis.

Factor analysis is a mathematical technique for reducing a complex system of correlations into fewer, more manageable dimensions. This analysis derives composite variables in a mathematically direct fashion by taking linear combinations of the original variables (Harris, 1975). Geometrically this may be viewed as placing axes through n dimensional space, where n is equal to the number of ecological variables. The first factor has the maximum averaged squared correlation with the variables in the set, so it is the axis that resolves the greatest proportion of the variation. Since the square of the correlation coefficent is a measure of the variance predicted by the variables examined, it is possible to state the amount of variance for which a factor accounts. The second axis is placed perpendicular to the first and resolves the greatest amount of the variance remaining after the placing of the first factor. Each successive factor will account for smaller amounts of the total variance. Placing factors continues until a sufficent level of the variation of the original variables is expressed in the factors. The procedure thus achieves a considerable simplification, at the cost of minimal loss of information (Gould, 1981).

For every ecological variable the factor analysis provides a "loading" value. The loading value represents the extent to which that variable contributes to the variation of the constructed factor. The loadings range from −1 to +1, so they

can be interpreted simply as the farther away from zero, the greater the importance that variable has in the factor. The factor also provides an eigenvalue for each factor. This value can simply be interpreted as the variance for that factor (Gouzoules, 1981). Only those factors which had an eigenvalue greater than 1 were considered significant.

In order to simplify the definition of the factors an "Orthogonal Varimax Rotation" was carried out on the ecological data. This rotation maximizes the variance of the squared loadings in each column. This method of rotation is most widely used and thus allows comparisons to be made more easily.

It was necessary to compare the individual score for each quadrat on each factor. The individual score was calculated as the quadrat's score on each ecological variable, multiplied by the loading of that variable on the factor, divided by the eigenvalue of that factor, summed over all variables in the set composing that factor. The standardized score of a variable was calculated as the distance from the mean of all subjects divided by the standard deviation of the variable (Nie et al., 1975).

The SPSS factor program (Nie et al., 1975) was used to calculate the factor analysis. The factor analysis produced four factors with eigenvalues of greater than 1. These four factors accounted for 79% of the variation in the original 20 ecological variables. Table 5 gives a description of each factor, the variables which load highly and their loading.

The factors developed are mathematical constructs; they are not real entities. Extreme caution must be used when applying biological meaning to strong factors (Gould, 1981). A claim of biological meaning cannot be based upon the mathematics alone, additional knowledge of the system under study is required. Since the factor analysis performed on the ecological variables produced strong factors and since the system under study is well known, a fairly strong argument can be put forward supporting the heuristic labelling of the factors listed here. The first four factors account for a high level of the variation (79%). Not only does each factor contain a small number of variables which load highly to it, but the manner in which the variables combine to form

Table 5:
The four major ecological factors, listing those variables with high loadings. (% of the variance in the ecological variables they explain)

Factor 1 (42%) (Food Species Providing Cover)		Factor 2 (15.5%) (Open Areas with Edge)	
Food Density (med)	0.88967	Plant Diversity (low)	0.89660
Cover	0.88544	Plant Density (low)	0.87329
Food Diversity (med)	0.83275	Plant Diversity (high)	0.74967
Food Diversity (low)	0.72255	Human Disturbance	0.56132
Area Covered	0.67747		
Food Diversity (high)	0.66474		

Factor 3 (11.3%) (Dense Vegetation)		Factor 4 (10.1%) (Food Plant Density)	
Plant Density (high)	0.88789	Food Density (high)	0.97463
Phenology	0.85591	Food Density (low)	0.93016
Plant Diversity (med)	0.80812	Area Covered	0.24426
Area Covered	0.43797		

the factors makes intuitive sense.

The first factor loaded strongly to characteristics of food plants which provide cover for the vervets and was labelled "food species providing cover". The medium sized plant density and diversity variables, as well as the cover variable loaded strongly (>0.08). This factor accounts for 42% of the total variation in the ecological variables examined. Factor two is loaded highly with the characteristics of open areas which have a high level of human disturbance, but also they load highly with diversity of tall plants. These variables would seem to represent the open areas of secondary growth which are surrounded by tall plant species. This factor, which accounts for 15.5% of the variation in the ecological variables, was labelled "open areas with edge". The third factor is loaded highly with variables which are characteristic of densely vegetated areas, and accordingly was labelled "dense vegetation". It accounts for 11.3% of the variation in the ecological variables. The last factor is only loaded highly by food density of tall and small plant species. These two variables alone account for 10.15% of the variation in the ecological variables. This variable is termed "food plant density".

IV. BEHAVIOURAL ECOLOGICAL RELATIONSHIPS

This chapter will describe the statistical analysis of the differences in the behaviours of the vervet study group in different areas of their home range. The four factors that were outlined in the previous chapter were used in this analysis to represent the different ecological conditions. The statistical description of the relationships between the ecological conditions and the group's behaviour was conducted in two ways. First, a regression analysis was preformed. For the purpose of the regression analyses each quadrat became a "subject", with a score for the frequency and duration of each behaviour and a score for each of the four ecological factors. Because the ecological factors are statistically derived compositions, each containing contributions from all the ecological measures, it is not suitable to use them as independent variables and look for combined effects. Therefore, in this analysis each ecological factor was designated as the dependent variable in a regression equation where behaviours were inserted as independent variables. In this way, equations illustrated which combination of behaviours best predicted each ecological factor. In as much as the heuristic interpretation of the ecological factors are valid, the equations allow us to suggest relationships between qualities of the habitat and the expression of behaviour. The r values produced by this analysis depicted the strength with which the frequency and duration of the behaviours were related to each of the four factors. The mean frequency and duration with which each behaviour was exhibited in a quadrat was used in further analyses in order to compensate for the fact that different quadrats had different numbers of focal animal sessions. Only those quadrats in which more than 10 focal animal samples were conducted were used in the regression analysis. This resulted in comparisons being made between 24 quadrats.

The second statistical method used to describe the relationships between the behavioural variables and the ecological factors involved an analysis of variance. Mean frequencies and durations were calculated for each behaviour in every quadrat, and then for both the frequency and duration independently, quadrats were placed into a high, medium or low group based upon the

characteristics of the behaviour. The variance of the ecological factor in each of the three categories were then compared using an analysis of variance.

The regression analysis revealed the greatest amount of information since it did not depend on comparing three groups, but compared all entries. However, if the relationship was not totally linear, the analysis of variance revealed important information. For example, the analysis of variance revealed instances where the medium group was significantly higher than the low group, but not significantly higher than the high group category. This sort of situation would not have been easily interpreted from a regression analysis. In addition the analysis of variance was relatively easy to interpret and represent.

A number of behaviours were observed to occur only rarely, for those behaviours the sample sizes were often so low as to restrict the probability of producing significant results. When possible, some of the behavioural categories were combined with similar behavioural categories. This effectively increased the sample sizes. For example, a behavioural category called agonistic behaviours was formed by combining "headbob", "bodybounce", "open mouth threat", "bite", "grab", "cuff", "branchshaking displays", and "chase attack" sequences into one category. The combined categories are presented in Appendix 1.

Neither the regression analysis or the analysis of variance produced significant results for the first factor, called "food plant species providing cover". The lack of interrelationship between this factor and behaviour can largely be explained by the nature of the factor. The ecological variables which load highly into this variable are not localized to any one particular area, consequently, a high proportion of the quadrats are highly related to this factor. Thus, it is suggested that this factor represents ubiquitous conditions found throughout the group's home range. Because this factor represents such a wide spread composition of ecological variables it is unlikely that the monkeys' behaviour would be specialized to it. The ubiquitous nature of this factor is supported by the fact that so many variables load highly into it. Six ecological variables

loaded into this factor at a level greater than 0.500. This factor represented too broad an ecological condition for the vervets to differentially respond to it.

The second factor, open area with edge, was significantly related to a number of the behaviours analysed. Factor two explained 15.5% of the variation in all of the ecological variables. This factor was strongly negatively correlated with the frequency of feeding behaviours ($r=-0.481$, $P=0.009$), and weakly positively with the duration of a feeding bout ($r=0.318$, $P=0.065$, Table 6,7) This suggests that as an area progressively becomes more open and possesses more edge, that the vervets respond by foraging less often, but when foraging occurs it is typically for longer periods of time. This relationship was also expressed as a trend in the analysis of variance, however, it did not reach a 0.05 significance level. The relationship may be explained by the fact that some of the most preferred fruiting trees, such as clammy cherry trees, were often found on the edge of clearings. Since clammy cherries were one of the most desired food species, whenever an animal fed in these trees they would do so for a long time. It was not uncommon for an individual to be engaged in feeding for a whole focal animal session of five minutes while in these trees. Contrary to what was first expected, there exists a strong correlation between grooming, both frequency ($r=0.371$, $P=0.036$) and duration ($r=0.525$, $P=0.004$) and the open area with edge factor. Grooming bouts did occur in open areas, such as in pastures, however it was my impression that they were relatively rare and typically of short duration. However, long bouts of grooming were frequently observed to occur under the trees which were immediately adjacent to the open areas. I suggest that it is the influence of these edge areas that is the major cause of this significant relationship.

The general impression received was that the vervets tended to rest longer in quadrats which scored highly on the open area with edge factor, although this relationship did not reach a 0.05 level of significance ($r=0.213$, $P=.128$; $F=3.206$, $P=0.061$). This could indicate a tendency for the vervets to rest for longer durations while sitting under the fruiting trees at the edge of the open areas. There is no indication that the frequency of resting is related

to this factor (Table 6,7)

The frequency with which affiliative behaviours were expressed was significantly related to this factor (r=0.396, P=0.028). However, the duration of these behaviours was not significantly related (r=0.227, P=0.143). Since affilative behaviours do not commonly occur over any long duration, duration may not be a very meaningful measure. Agonistic behaviours produced the exact opposite situation. Duration was significantly related to the factor (r=0.405, P=0.025), but frequency was not (r=0.291, P=0.084). This relationship may relate to the fact that fights in the fruiting trees on the border of the open areas often involved long chases. Also, it was not uncommon to see long chases in the open areas themselves. Males would frequently chase other males across the pasture.

It has commonly been suggested that primate species that live in open areas, such as savannas, experience higher risk of predation than forest primates (DeVore, 1963; Gartlan, 1968). This suggestion can be tested by actually quantifying the risk of predation, or more realistically, by quantifying the frequency with which predator avoidance occurs, assuming that predator avoidance is a good measure of actual risk of predation. If this prediction is true, it would seem logical to expect that attention or surveillance behaviours occur more frequently in open areas. In this study neither the vervets' rate (r=0.177, P=0.205) nor their duration (r=−0.204, P=0.169) of attention behaviours, were related to the open area with edge factor.

Animals were observed playing 125 times during the study. The duration of play bouts varied from a couple of seconds to the full five minute focal animal session. Play was positively related to the open area with edge factor (r=0.0503, p=0.006) The relationship that was revealed between play duration and a quadrat's level on this factor is difficult to interpret. The regression analysis showed that these variables were not significantly related (r=0.255, P=0.115). However, the analysis of variance shows that play bouts were of significantly shorter duration in quadrats which scored low on this factor than in the middle ranked quadrats but not high scoring quadrats (F=5.37, P<0.01) The mean score on this factor for the ranks are: 0.601 low, 1.550 medium, 0.952

high. The medium group was significantly different from both the low and high groups (Scheffe<0.05), but the high was not significantly different from the low group (Scheffe>0.05). This demonstrates a slight bell shape to this relationship. Possibly this suggests that there is a trend for play bouts to increase in length as the habitat becomes more open until a certain critical level is reached where upon the duration starts to decrease.

Multiple regression analysis can analyse the relationship between a dependent variable, in this case the open area with edge factor, and a set of independent variables, in this instance behaviours. It will generate the best linear predictive equation composed of the various independent variables, stating the amount of variation in the dependent variable each independent variable accounts for. The stepwise regression equation performed for the open area with edge factor is composed of three significant variables. These three variables alone are capable of explaining 49% of the variation in this factor. The first variable to go into the equation is the duration of grooming which accounts for 27.5% of the variation in the open area with edge factor. When the next variable, the frequency of affiliative behaviour, is added into the equation a total of 37.6% of the variation is accounted for. When the final variable, rest frequency, is included, 48.7% of the variation is explained. This procedure clearly demonstrates the tendency for the vervets to use areas which are very open and contain edge for the frequent expression of resting and affiliative behaviours and long grooming bouts. The opposite situation also is true, in closed areas with little edge, resting and affilative behaviours rarely occur and grooming bouts tend to be short. The regression analysis clearly verifies the importance of this factor for the frequency of resting. This was not fully realized in the previous analysis.

The analyses examining the relationship between the vervets' expressed behaviour and the third factor, called "density of vegetation", revealed some interesting results. Since dense vegetation would seem to be a fairly safe place for a terrestrial primate, one might expect a positive correlation between this factor and resting and grooming; also a negative correlation would be expected

with attention. The actual results in no way support these predictions.

There is no significant relationship between this factor and either the frequency or the duration of resting, nor the frequency or duration of grooming (Table 6,7). The analysis of variance similarly produced no significant results. In contrast, both the frequency (r=0.533, P=0.004)and duration (r=0.4886, P=0.008) of attention were significantly positively correlated with density of vegetation. Simply stated this means that the vervets did not rest or groom longer or more frequently in densely vegetated areas, but they did exhibit significantly more and longer attention behaviours.

An animal was considered to be exhibiting attention behaviours whenever it was observed to be in a state of vigilance observing its environment. This behaviour was either directed at conspecifics, especially when they were engaged in agonistic interactions, or at potential predators. It was often not possible to conclusively state what the subject was directing towards. It is suggested that this behaviour should relate to the degree of anxiety of an animal, the more uneasy an animal is, the more you would expect it to be attentive to its environment. Quadrats ranking high, medium or low on this factor did not significantly differ in their frequencies (F=0.250, P=0.781) or durations (F=0.383, P=0.687) of agonistic behaviours. It would appear that the increased level of attention is not caused by an increase in the amount of attention behaviour directed to conspecifics engaged in agonism. It could be possible that it is in these areas that the vervets are most concerned about the possibility of predation. Since humans are a major predator of vervets on St. Kitts, and since the level of human disturbance of those quadrats in which attention was given at the lowest frequency was not significantly different than quadrats having higher frequencies (t=0.8062, P>.10) it seems unlikely the association between attention and density is related to human predation. It could be that since in dense vegetation visibility is reduced, in order for an animal to have adequate awareness of what is happening in the immediate area, the animal must be monitoring its environment more frequently. If a disturbance does occur in dense vegetation, one would expect that it would take longer to identify its

origin, or if it was an agonistic encounter, to identify the participants. Also, it is possible that since visibility is limited in densely vegetated areas that the animals were just more obviously attentive in these areas. In the open areas they may have been just as attentive as in densely vegetated areas, but here the animals could monitor all dangers without exhibiting the obvious signs that they were efficiently monitoring the environment. On a number of occasions when the group was in open areas, they would respond to people when they first became visible at a distance of over 200 meters.

The conditions causing this increased level of vigilance may also be expressed in other behaviours. The frequency ($r=-0.338$, $P=0.050$) and duration ($p=-0.384$, $P=0.032$) of play are both negetively correlated with this density of vegetation factor, as is the duration of affilitive behaviours ($r=-0.354$, $P=0.045$). Thus, in densely vegetated habitats play occurs proportionately less often than in less dense habitats and when it does occur it is of short duration, also affilitive behaviours tend to be of short duration in dense habitats.

The last significant result produced in the analysis of this factor demonstrated that the vervets tended to feed more frequently as habitats become progressively denser ($r=0.579$, $P<0.001$). Since there are no significant positive relationships between any of the behaviours examined, except attention, it seems reasonable to speculate that the main reason the vervets are using densely vegetated areas is to feed.

The regression equation generated to express the relationship between behaviour and factor 3 exhibits a fairly high overall accuracy of prediction. Three variables are included in this equation which have an F value with a probability less than 0.05. These three variables account for 57.5% of the variation in the density of vegetation factor. The first behavioural variable to go in the equation is the frequency of feeding ($R^2=0.335$). When the next variable, the frequency of attention behaviours, is added to the equation a total of 47.6% of the variation in this factor is accounted for. The last variable to be added is the duration of play, which brings the level of explained variance up to 57.5%. In order to interpret this equation it must be remembered that play

correlates negatively with this factor. The high accuracy level of this prediction equation demonstrates that the vervets tended to feed frequently in densely vegetated areas while often surveying the environment but played rarely and if they did, it was for a short time. The opposite is also true, that in areas that were sparsely vegetated, play occurred in long bouts and the frequency of feeding and attention behaviours were low.

The food plant density factor was the last to be analysed. This factor explained 10.1% of the variation in the ecological variables, however not many of the behavioural variables were significantly related to this factor. Contrary to what might be expected, this food plant density factor was not significantly related to either the duration of feeding ($r=-0.007$, $P=0.488$), nor the frequency of feeding ($r=0.198$, $P=0.176$). This would suggest that the vervets are making an active selection of those plant species to be eaten based upon characteristics of plants other than plant abundance. The frequency ($r=0.666$, $P<0.001$) and duration ($r=0.384$, $P=0.032$) of affiliative behaviours and the frequency of agonistic behaviours ($r=0.338$, $P=0.050$) are all positively correlated with this factor. Simply stated this relationship suggests that when food plant density is high the vervets expressed long duration affiliation bouts frequently and had a lot of agonistic bouts. The reverse is also true. This could be interpreted to suggest that, when the vervets were in areas which were characterized by high densities of food plants, there was competition over the food. This is evident in the high frequency of agonistic behaviours. A possible reason that affiliative behaviours occurred so frequently in high plant density areas, is that they would counteract the aggression which occurs here frequently.

None of the remaining behaviours were related to the level of the food plant density factors (Table 6,7).

Only the frequency of affiliative behaviours entered into the regression equation with an F probability value which was less than 0.05. This behaviour alone accounted for 44.1% of the variation. If the speculation concerning the relationship between agonistic and affiliative behaviours is correct, then this high

R^2 value would suggest that the unit increase in affiliative behaviours was much greater than the unit increase in agonistic behaviours. This means as the level of agonistic behaviours rose slightly in response to an increase in food plant density, the frequency of affiliative behaviours rose drastically. The reason why the duration of affiliative behaviours failed to enter significantly into the regression equation may have to deal with the natural constraints of the behaviour. Some of the behaviours within the affiliative behaviour category are just as effective at signalling intention when given in short duration as when given in longer durations.

The major objective of this chapter was to statistically investigate the behavioural response of the study group to changing environmental conditions. The analysis resulted in the illumination of several significant and meaningful relationships (Table 6). In addition, no support was found for a number of the behavioural ecological relationships that have been suggested in the past.

The proposition that high levels of cover decreases the chance of predation and favors the expression of less attention behaviour and more behaviours such as play and grooming, is not supported. The vervets studied here expressed almost the exact opposite; social behaviours such as grooming and play occurred significantly more often and longer in areas that were relatively open, and attention behaviours were expressed the most often and for the longest periods in areas where cover was high.

Chalmers (1968) speculated that aggressive behaviour should negatively correlate with food availability. Presumably, this speculation stemmed from the idea that in primate social groups there will be increased competition over scarce food resources. This study of the St. Kitts vervet demonstrated that the highest frequency of agonistic behaviours occurred in those areas where food plants were the most abundant. If competition was occurring in these areas of abundant food, it is not likely stemming from the increased availability of food resources. There would be no advantage to compete over access to abundant resources. It might have been predicted that the vervets would forage most in

Table 6: F Test values examining the relationships between factors and behaviours
F Value / Probability

BEHAVIOUR		FACTOR 1	FACTOR 2	FACTOR 3	FACTOR 4
Play	Fre	0.30/0.74	3.35/0.05	1.82/0.19	0.10/0.91
	Dur	0.23/0.80	5.37/0.01	2.60/0.10	2.37/0.12
Feed	Fre	0.19/0.83	1.15/.034	15.5/0.00	0.32/0.73
	Dur	0.35/0.72	1.04/0.37	0.69/0.51	0.64/0.54
Attention	Fre	0.12/0.89	0.32/0.73	11.3/0.00	0.44/0.65
	Dur	0.43/0.66	0.86/0.44	2.60/0.10	0.62/0.94
Agonism	Fre	0.14/0.87	1.06/0.36	0.25/0.78	2.56/0.10
	Dur	0.78/0.78	14.6/0.00	0.38/0.69	0.06/0.94
Groom	Fre	1.28/0.30	1.05/0.37	1.76/0.20	1.45/0.26
	Dur	0.06/0.94	6.29/0.01	0.97/0.40	0.13/0.88
Rest	Fre	0.21/0.81	0.97/0.40	0.85/0.44	1.02/0.38
	Dur	1.82/0.19	3.21/0.60	1.01/0.38	1.82/0.19
Affiliative	Fre	0.10/0.90	2.39/0.11	0.20/0.82	12.8/0.00
	Dur	0.16/0.85	2.13/0.15	0.71/0.50	1.97/0.17

Fre = Frequency Dur = Duration

Table 7:Correlation values describing the relationship between factors and behaviours
r Value / Probability

BEHAVIOUR		FACTOR 1	FACTOR 2	FACTOR 3	FACTOR 4
Play	Fre	-.19/0.18	0.50/0.01	-.34/0.05	0.05/0.41
	Dur	-.19/0.19	0.25/0.12	0.38/0.03	0.04/0.43
Feed	Fre	0.01/0.48	-.48/0.01	0.58/0.01	0.20/0.18
	Dur	0.12/0.29	0.32/0.06	-.14/0.26	-.01/0.49
Attention	Fre	0.20/0.18	-.18/0.21	0.53/0.01	-.10/0.31
	Dur	-.09/0.35	-.20/0.17	0.49/0.01	-.14/0.25
Agonism	Fre	-.10/0.32	0.29/0.08	-.20/0.18	0.34/0.05
	Dur	-.27/0.11	0.40/0.03	-.28/0.09	-.01/0.48
Groom	Fre	0.25/0.12	0.37/0.04	-.15/0.24	0.10/0.31
	Dur	-.01/0.49	0.52/0.01	-.30/0.08	-.03/0.44
Rest	Fre	0.06/0.39	0.07/0.38	-.10/0.32	0.14/0.26
	Dur	0.03/0.44	0.21/0.13	-.31/0.07	-.01/0.48
Affiliative	Fre	-.12/0.28	0.40/0.03	-.12/0.30	0.66/0.01
	Dur	-.15/0.24	0.23/0.14	-.35/0.05	0.38/0.03

Fre = Frequency
Dur = Duration

those areas which have the highest density of food, however, this was not observed. This suggests that the vervets are either selecting foraging areas on the basis of something other than food abundance (possibly food quality), or that they were avoiding the areas of high plant density for some unknown reason. This study revealed the significance of relationships that have not been previously expressed in the literature. For example, it was demonstrated that the vervets of this study expressed affiliative behaviours more frequently and longer in both open areas with edge and in areas possessing high food plant density. They also tended to rest longer in the edge of open areas. The large number of behaviours which were significantly related to the open area with edge factor would seem to support Kavanagh's (1980a) claim that the vervet monkey is adapted to exploit newly created secondary growth environments. Areas which loaded highly to this factor were typically areas which were recently disturbed.

Even though significant relationships between the group's ecology and its behaviour were substantiated, caution should be used in applying these results beyond the scope of this study. There remains a large amount of unexplained variation that must be examined before generalizations are made. I suggest that it is probable that a large proportion of the remaining variation would be explained by examining social factors, in addition to ecological conditions.

V. DIFFERENTIAL RANGE USE

Reasonably accurate density estimates of the study group in different areas of its home range were necessary for comparisons to be made between the intensity with which an area was used and the ecological conditions of the area. Density estimates of primate populations are often lacking, or if researchers do provide an estimate, the method by which it was calculated is rarely described (Wilson and Wilson 1974). The most commonly used method to obtain reliable primate population censuses, apply some form of transect technique (see Southwick and Siddiqi, 1966; Southwick and Cadigan, 1972; Wilson and Wilson, 1974; Green, 1978). Transect methods are also often employed in estimating the size of a variety of animal species populations, so discussions of the accuracy of various methods have been published (see Davis and Winstead, 1980; Seber, 1982; Blaine et al., 1981). Following established methodology, estimates of the population density of the vervets in the areas censused by the 12 transects were compared (as previously outlined).

Over the whole 8 month study period, the 12 transects were walked at least 10 times in each daylight hour for a total of 1462 transects. The transects varied in their total length from 95m to 540m and the average length was 240m. The animal density for each transect (calculated as per the formula previously outlined), resulted in strikingly different values for the different transects. The population density for the transects varied from 400 individuals per km^2 in the pasture transect, to 1 individual per km^2 in the slope transect which was dominated by grass. Of the total number of animals seen throughout the duration of the study in all transects, 57% were seen in only 3 out of the 12 transects. This extreme variation between density estimates of the different transects illustrates that the vervets are differentially exploiting the habitats available to them. This suggests that the animals are actively selecting the habitats which they use. The population densites of the transects are illustrated graphically in Figure 6.

The count obtained by using this transect census technique can be used to calculate the total population in the area. In order to obtain an estimate of

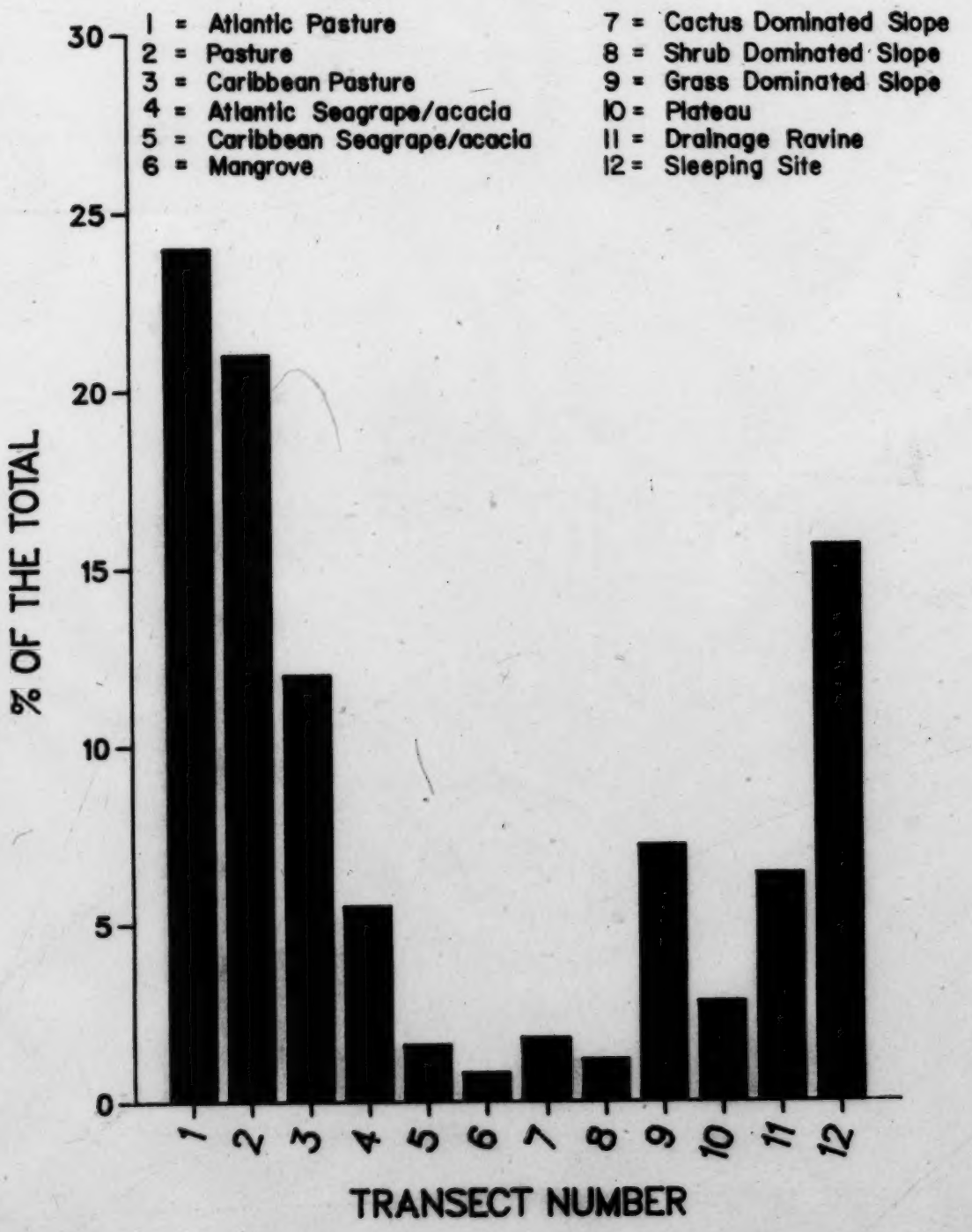


Figure 6: The percent of the total number of monkeys seen on the different transects.

the population in the area sampled, the total number of animals seen was divided by the total area sampled and the number of times it was sampled. This produces a population estimate of 114 individuals per km². Since both the home range size and the group size of the study group are known, a more reliable estimate of the vervet population density can be produced simply by dividing the group's size by its home range size. This method produced a population density estimate of 90.0 individuals per km². The difference between the two methods illustrates the inaccuracy of the transect methods in estimating the size of the study population. This inaccuracy in the transect methods, does not influence the validity of comparing population estimates of the different transects, since each transect was censused in the same fashion and to a similar level of accuracy.

Since it was possible to determine the ecological characteristics of the area included in each transect, it is possible to relate the population density of a transect to its ecological characteristics. A regression analysis was performed between each transect's standing on each of the 20 ecological variables and its respective population density estimated from transects walked at all times of the day. In addition, a similar analysis was performed using the census data collected at different times of the day. From this additional analysis, interpretations were made of the diurnal variation in habitat use. For the purpose of this analysis the daylight hours were divided into four periods; early morning, (dawn to 9AM); late morning, (9AM to noon); early afternoon, (12PM to 3PM) and late afternoon, (3PM to dusk).

In the analysis using transects from all hours of the day it was found that the use of the group's home range was not significantly related to any of the ecological variables, with the exception of the plant diversity and density variables. In particular, the population densities were related to the density ($r=0.445$, $P=0.056$) and diversity ($r=0.489$, $P=0.038$) of tall food plants, as well as the diversity of all tall plants ($r=0.579$, $P=0.015$). These high r values suggest that through the entire day the vervets were preferentially associating with habitats which contained large plant species. The only other significant

variables which the population density related to for the whole day was the diversity of small plants (r=0.542, P=0.023) and to a lesser degree small food plant diversity (r=0.390, P=0.084).

In the regression equation generated to examine these relationships, only two variables had an F value with a probability of less than 0.05, so as to enter into the regression equation. The tall plant diversity variable entered the equation first and explained 34% of the variation between the population densities of different transects. The diversity of small plants was the second variable to enter into the equation and it resulted in an accumulated variation of 71% of the variation being explained. This regression equation is relatively powerful, thus it can conclusively be stated that throughout the day, the vervets in the study group selected areas which had high small plant and tall plant diversities. These conditions most commonly occurred in transects which contained more than one habitat type, such as the pasture transect, which in addition to including pasture, included a border of tall fruiting trees. In these areas foraging often occurred in both the open areas and in the tall fruiting trees and the most common location for the vervet to rest was under these trees at the border of the open areas.

An analysis of the distribution of population densities of the transects in the early morning revealed a strong correlation between the population density of the transects and tall food plant density (r=0.755, P=0.001) and diversity (r=0.624, P=0.009) and tall plant density (r=0.981, P=0.000). Also the vervets more frequently used areas which scored higher on the phenology variable (r=0.514, P=0.030).

The regression equation generated for the early morning population distributions explained an extremely high amount of the variation. Tall plant diversity was the first variable to enter into the equation and alone it explained 96.2% of the variation in the population densities. This extremely high R^2 value indicates that in the early morning the vervets were selecting areas primarily based upon the area's tall plant species diversity. The second variable to significantly enter into the equation is the diversity of small plants, which

resulted in an accumulated R^2 value of 0.9830. Following this, the variable called "food area covered" entered into the equation. These three variables explained 99.3% of the variation in population densites between transects. The high R^2 value would indicate that in the early morning the vervet's choice of areas depended almost entirely upon the selection for the level of plant diversity of the area. Since in the early morning the major activity is foraging, this selection is what would be largely expected, for in these areas foraging could be done efficiently.

In the late morning, between 9AM and noon, the vervet's population density was correlated with a number of variables. There was a strong tendency for transects characterized as areas with high levels of human disturbance to have high population densities ($r=0.631$, $P=0.008$). Also, there was a significant negative correlation between cover and population density ($r=0.517$, $P=0.029$). There existed a very strong positive relationship between the density of vervets in an area, and the density of small sized plants ($r=0.801$, $P=0.000$) and a less significant relationship existed between transects containing mostly medium sized plants ($r=0.431$, $P=0.062$) and the animal density of the transect. The only other relationship that approached significant levels, was between the diversity of tall food plant species and the population density of an area ($r=0.421$, $P=0.067$). Even though a large number of variables related to the population densities of the transect at this time of the day, only two variables entered into the regression equation, the density ($r=0.642$) and diversity ($r=0.824$) of small plants. This would indicate that the vervets were selecting open areas, such as the pasture, since this area had both the highest density and diversity of small plants of any transect. I suggest that this selection is related to the tendency of the vervets to rest under the trees at the edge of open areas. This is supported by the high positive correlation to both open area charcteristics and the diversity of tall plants.

In the early afternoon, between noon and 3PM, the population density of the vervets was only correlated to the density ($r=0.488$, $P=0.038$) and diversity ($r=0.488$, $P=0.038$) of tall food plants. This would appear to be an anomaly,

since the vervets are not feeding at this time, they are resting. However, this can be explained, because in the areas in which the vervets normally found themselves at this time of the day, all of the tall trees are fruiting trees.

No variable had an F value with a probability of less than 0.05, so no regression equation was generated for this time of the day. This cannot be taken to imply that vervets were not in association with any one type of habitat since at this time of the day, very few animals were sighted in any transect. In five out of the 12 transects no animal was even seen at this time of the day.

At the end of the day the population density of the study group was found to be related to a number of ecological characteristics of the transects. As in early morning, there was a significant positive correlation with the level of human disturbance and the population density ($r=0.479$, $P=0.042$). This may be related to the fact that at this time of the day the vervets commonly spent a lot of time foraging, and areas with high levels of human disturbances tend to have a large proportion of secondary growth plants, which are a desired food source of the vervets. It may be the selection for these secondary growth areas that causes a significant relationship to exist between the density of small plants and the transect's population density ($r=0.457$, $P=0.050$). The selection of areas in order to facilitate foraging is further substantiated by the fact that there is a significant correlation between both tall food plant density ($r=0.515$, $P=0.030$) and tall food plant diversity ($r=0.727$, $P=0.002$)

Only the diversity of tall food plants entered into the regression equation for this time of the day. The tall food plant variable alone explained 53% of the variation in the transect's population density.

Habitat selection is simply the selection of a type of place with which to associate (Partridge, 1978). It is often intuitively apparent that animals are found in a more or less restricted range of their environment. It is less obvious on what basis the animals select to restrict their distribution. In the

analysis of the distribution patterns of the vervets observed in this study, it was demonstrated that they were actively selecting the areas they were using. It would appear that this selection was to some degree, based upon the ecological characteristics of the areas. Throughout the entire day the vervets were preferentially selecting areas which had high plant diversity. If the day is subdivided, the distribution of vervets illustrates the selection of habitats which are suitable to the behaviours with which they engage in at that time of the day. The distribution of the vervets revealed a strong association between heavily used quadrats and areas of secondary growth. This association supports the claim that the vervet monkey is a colonizing species, specifically adapted to secondary growth areas (Kavanagh, 1980a).

Significant emerging patterns of range use can only partially be explained by selection for the specific ecological conditions examined. For example, the analysis does not explain why the study group would not forage or rest in the drainage ravines of the hill, which provided clumped food resources and cover, while they would select very ecologically similar areas in the flat bay area. It did not explain why the group would select a sleeping site which was over 800m from the areas which were most intensively used, when other ecologically similar areas, closer to the core areas, were available. This suggests that the vervets were selecting areas based upon either ecological factors that were not examined, or possibly upon behavioural conditions, such as past experiences in an area.

VI. DISCUSSION

The major objective of this research is to quantitatively investigate the basis upon which the vervet monkeys under study are selecting habitats, and what behavioural responses they show. In order to meet these objectives the investigation concentrates on three areas: (1) a general discussion of the behaviour and ecology of the study group; (2) an analysis of how the expression of particular behaviours (frequency and duration) are related to specific ecological conditions; (3) an analysis of the ecological basis of the vervets' selection of habitats.

The vervets were associating with those habitats which had high diversity of tall and small plant species. This condition most commonly occurred in areas which contained more than one habitat type. The quadrats with the highest level of both tall and small plant diversity were composed of pasture which was bordered by tall fruiting trees. These ecological conditions are what are described by the factor labelled "open area with edge". Because the areas of high use are also those which can best be described by this factor, it is possible to state the influence that the preferred areas have on the behaviours of the study group. In these areas vervets exhibited more and longer play, groom and affilitive behaviours and when they rested here, they did so for a longer duration.

The increased frequency of social behaviours, such as grooming and play in open areas, and the fact that attentive behaviours only showed significantly increased levels in habitats which were characterized as having dense vegetation, is evidence in opposition to the claim that in open areas animals are under greater predation risk. Curiously enough, the areas which are preferentially being selected are also the areas which are characterized as having the highest level of human disturbance, and are also the areas where dogs were most often seen. Thus, it would seem reasonable to suggest that these preferred areas are also the areas where the probability of predation is the greatest. This seem

paradoxical, for it would appear to be adaptive to avoid areas where the risk of predation is high. I suggest that these areas provide the monkeys with benefits which outweigh the increased risk of predation.

Altmann and Altmann (1970) found that baboons in Kenya tended to associate in areas that were the most dangerous, as judged by the number of reactions to predators which the baboons expressed while in the areas. This would suggest, as does the similar observations found in this study, that predators may not have very strong influence on the movement of a group about its home range. In this study, this cannot be attributed to any lack of predator pressure, for on several occasions attempted predations on the study population by hunters with dogs were directly observed. Both of the neighboring groups lost members to human hunters. A feral dog pack was also observed to hunt the monkey population in the study area, but no successful predation was seen.

The evidence suggests that the vervets are preferentially selecting pasture areas which are bordered by tall fruiting trees, these are areas of high human disturbance and thus have a large amount of secondary growth. It is also these areas which load most highly to the open area with edge factor and it is this factor which is associated with the majority of the behavioural ecological relationships discovered here (Table 6).

The nature of secondary growth areas are poorly understood. Few quantitative investigations have been made of border areas, and even fewer of them in tropical habitats which are inhabited by primates. The nature of the tree fall is one of the most intensively studied areas of secondary growth in tropical systems. Within the area of a recent tree fall, Hartshorn (1978) identified a tremendous increase in the diversity of plant species in comparison to the surrounding undisturbed forest. Not only were the majority of species commonly found in undisturbed forest present in the tree fall, but species specifically adapted to areas of secondary growth were also present. These findings are supported by the results in this study. Those quadrats which contained these secondary growth border areas had the highest level of

diversity in all size classes of plants. Whitmore (1978) discovered that tree fall gaps in Costa Rican forests were occupied by up to 80 different tree species. Webb et al. (1972) described the events that occurred over 14 years following the experimental clearing of rain forest areas in Queensland. They discovered that leaf biomass production in the experimentally cleared areas rose rapidly following clearing to surpass the leaf production of the control areas. The fruit production of the experimentally cleared areas also rapidly increased so that in seven years fruit production was only slightly less than that of the control area. This suggests that the selection of these secondary growth border areas may be associated with the selection of areas of increased productivity. This is supported by the fact that when the vervets foraged in these areas, they did so for a significantly longer duration.

It is also possible that the vervets are selecting these secondary growth border areas because these areas have a higher proportion of their net primary productivity available to consumers, than do undisturbed areas. In areas which are undisturbed, the plants may be investing a large proportion of their energy in the production of wood, which is to a large extent unavailable to predators, whereas, areas of secondary growth are putting proportionately less energy into the production of wood. A second characteristic of areas of secondary growth which might influence the quality of the forage available deals with production of plant toxins. Janzen (1970, 1979) discovered that plant species inhabiting secondary forest patches invest less in predator defense, than primary rain forest plant species. Plants inhabiting areas of secondary growth are attempting to establish themselves in the areas and to out compete potential competitors. The most profitable strategy for a colonizing plant species in an area of secondary growth is to invest the majority of its resources in growth, so as to be more competitive for light. At this time in a plant's life, investment in predator defence mechanisms, such as toxins, are too costly (Janzen, 1970). Again, the speculation that the vervets are preferentially selecting these areas in order to have access to the higher quality food plant species is supported by the fact that when the vervets foraged in the secondary growth areas, they did

so for longer durations.

The few studies that have been conducted which examine areas of secondary growth in tropical habitats, suggest that these areas have high plant diversity, a higher productivity, and a greater proportion of the productivity available for primate consumption. Other studies on vervets have demonstrated a similar high reliance on areas of secondary growth. Moreno-Black and Maples (1977) observed that the diet of a group of vervets in the coastal forests of Kenya was dominated (67%) by items from secondary growth areas. Other species of primates have similarily been shown to be dependent on secondary growth areas. Kano (1979) observed that the pygmy chimpanzee (Pan paniscus) is predominately found in areas of secondary growth, especially along the rivers. Charles-Dominique (1971,1977) suggested that the angwantibo (Arctocebus calaborensis) is confined to areas of regenerating forest, such as tree falls. He found that the distribution of the angwantibos coincided exactly with the occurrence of tree fall areas. If tree falls were rare, the angwantibos were absent.

Even if the vervets are selecting these secondary growth border areas because of the characteristics of the food plants available to them there, it does not explain why some social behaviours would be significantly influenced by the open areas with edge factor. One possible explanation for the difference shown in behaviours is that the border areas tend to have more microhabitats available for exploitation, than do neighboring areas. The vervets of the study group seemed to select some of these microhabitats along the borders of the open areas. In particular, a few very specific locations stand out as areas that were intensively used. Along the border of the pastures, stands of clammy cherry trees (Cordia obliqua) were occasionally found. The monkeys were frequently found under these trees during the heat of the day. Between about 8 AM. and 3 PM., the most reliable place to find vervets was under one of the stands of clammy cherry trees. While under these trees, the animals commonly engaged in grooming, or they simply rested. The strong association between these monkeys and this microhabitat along the border of

the pastures, would help explain the high frequency of long duration resting and grooming bouts and possibly also those of affiliative behaviour, since the majority of the affiliative behaviours were expressed between grooming partners. This may explain how the differences in behaviours are found in these areas, though why these areas elicit these behavioural responses remains largely unknown.

This study has demonstrated that the group of vervets observed exhibited concentrated use of a few selected microhabitats, yet it was also found that the group was very dispersed. This apparent contradiction can be understood when the nature of their dispersion is examined. Usually there existed a fairly stable core group, plus a number of peripheral adult and subadult males which were either solitary or in small groups. The size difference between these subgroupings resulted in any area heavily used by the core group being a preferred area for the group as a whole. However, the core group normally selected the preferred habitats, displacing peripheral animals, and as soon as the core group moved out of a preferred area, other animals would move in. Thus, it is evident that there existed a temporal partitioning of selected microhabitats. Moreno-Black and Maples (1977) demonstrated temporal partitioning of microhabitats in the vervet monkeys inhabiting the coastal forests of Kenya.

The model which has been presented here, in which specific behaviours are related to particular ecological conditions, does not attempt to be an all encompassing explanation of behavioural variation. It does attempt to furnish an explanation of some of the variability that exists in behaviours expressed under different conditions. This study can be regarded as an initial step towards a more complete understanding of how behaviour is influenced by ecology. There remains a large amount of behavioural variability exhibited by the vervet monkey study group, which has not been explained. This suggests that either ecological variables, which were not examined, or other non-ecological variables are influencing the behaviour of the group. This study was not able to examine many variables which could influence the groups behaviours, such as kinship, dominance, and individual relationships. Also there are social resources which

may be limiting to group members which have not been examined, such as the availability of mates. These social variables are likely to be just as significant predictors of primates behavioural variability as ecological variables. A research design that examined both social and ecological variables would be complex, however it should be able to explain more of the variation in behaviour than one that concentrated on one sort of variable, neglecting the others. The results of this study clearly illustrate the need to examine behavioural ecological relationships in a quantitative manner. Claims made from qualitative appraisals of the situation are simply not adequate. A number of the behavioural ecological relationships which this study revealed were not initially apparent from casual observations. It may prove desirable to re-examine some of the behavioural ecological claims that are so abundant throughout the primate literature, since the majority of them arose from qualitative assessment.

Extreme caution should be employed in drawing generalizations about the primate order from only a handful of studies, especially when comparisons involve more than one species. When comparing more than one species it must be remembered that the different species bring different sets of phylogenetic baggage.

This study substantiated the existence of characteristic patterns of behaviours which relate to specific ecological conditions. The investigation of behavioural ecological relationships is a useful tool needed to understand the variation in behaviour. It is hoped that future research will continue along lines developed here and in doing so follow a quantitative methodology.

VII. BIBLIOGRAPHY

Aldrich-Blake, F.P.G. 1970. Problems of social structure in forest primates. In: J.H. Crook ed. Social Behaviour in Birds and Mammals. pp.79-101. Academic Press, London.

Altmann, S.A. 1959. Field observations on a Howling monkey society. J Mammal. 40:317-330.

Altmann, J. 1974. Observational study of behaviour: Sampling methods. Behaviour 49:317-330.

Altmann, S.A. 1974. Baboon, space, time, and energy. Amer. Zool. 148:221-248.

Altmann, S.A. and J. Altmann. 1970. Baboon ecology. University of Chicago Press, Chicago.

Aston, E.H. 1960. The influence of geographic isolation on the skull of the green monkeys (Cercopithecus aethiops sabaeus). V. The degree and pattern of differentiation in the cranial dimensions of the St. Kitts green monkey. Proc. Roy. Soc., Lond. 151:563-583.

Baskin, D.R. and P.D. Krige. 1973. Some preliminary observations of the behaviour of an urban troop of vervet monkeys (Cercopithecus aethiops) during the birth season. J. Behav. Sci. 1:287-296.

Brain, C.K. 1965. Observations on the behaviour of vervet monkeys (Cercopithecus aethiops) Zool. Africa. 1:13-27.

Bramblett, C.A. 1980. A model for development of social behaviour in vervet monkeys. Devel. Psycho. 13:205-223.

Brown, J.L. 1964. The evolution of diversity in avian territorial systems. Wilson Bull. 76:160-169.

Chalmers, N.R. 1968. The social behaviour of free living mangabeys in Uganda. Folia Primatol. 8:264-281.

Charles-Dominique, P. 1971. Eco-ethologie et vie sociale des prosimiens do Gabon. Biol. Gabon. 7:121-228.

Charles-Dominique, P. 1977. Ecology and behaviour of nocturnal primates:

Prosimians of equatorial West Africa. Columbia University Press, New York.

Charnov, E.L. 1976. Optimal foraging: The marginal value theorem. Theor. Popul. Biol. 1:129-136.

Cheney, D.L. 1981. Intergroup encounters among free-ranging vervet monkeys. Folia Primatol. 35:124-146.

Clutton-Brock T.H. 1974. Primate social organization and ecology. Nature 250:539-542.

Clutton-Brock, T.H. 1977a. Some aspects of intraspecific variation in feeding and ranging behaviour in primates. In: T.H. Clutton-Brock editor. Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes. pp.539-556. Academic Press, London.

Clutton-Brock, T.H. 1977b. Methodology and measurement. In: T.H. Clutton-Brock editor. Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes. pp.585-589. Academic Press, London.

Clutton-Brock, T.H. and P.H. Harvey. 1977. Species differences in feeding and ranging behaviour in primates. In: T.H. Clutton-Brock editor. Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes. pp. 557-579. Academic Press, London.

Clutton-Brock, T.H. and P.H. Harvey. 1977. Primate ecology and social organization. J. Zool. 183:1-39.

Crook, J.H. 1965. The adaptive significance of avian social organization. Symp. Zool. Soc. Lond. 14:181-218.

Crook, J.H. 1970. The socio-ecology of primates. In: J.H. Crook editor. Social Behaviour in Birds and Mammals. pp.103-166. Academic Press, London.

Crook, J.H. 1972. Sexual selection, dimorphism and social organization in the primates. In: B. Campbell editor. Sexual Selection and the Descent of Man 1871-1971. pp.231-281. Aldine Press, Chicago.

Crook, J.H., J.E. Ellis and J.D. Goss-Custard. 1976. Mammalian social systems: Social structure and function. Anim. Behav. 24:261-274.

Crook, J.H. and J.S. Gartlan. 1966. Evolution of primate societies. Nature 210:1200-1203.

Davis, N.B. 1978. Ecological questions about territorial behaviour. In: J.R. Krebs and N.B. Davis editors. Behavioural Ecology. pp. 317-350. Sinauer Associates, Inc. Pub. Sunderland.

Davis, D.E. and R.L. Winstead. 1980. Estimating the numbers of wildlife populaton. In: S.D. Schemnitz editor. Wildlife Management Techniques Manual. 4th edition. The Wildlife Society, Washington.

Denham, W.W. 1982. History of the green monkeys in the West Indies. Part I. Migration from Africa. Journal of the Barbados Museum of History Society 36:211-228.

Denham, W.W. 1982. History of the green monkeys in the West Indies. Part II. Population dynamics of Barbadian Monkeys. Journal of the Barbados Museum of History Society 36:353-370.

DeVore, I. 1963. A comparison of the ecology and behaviour of monkeys and apes. In: S.L. Washburn ed. Classification and Human Evolution. pp.301-319. Aldine Pub. Co., Chicago.

Dunbar, R.I.M. 1974. Observation of the ecology and social organization of the green monkey Cercopithecus sabaeus, in Senegal. Primates. 15:341-350.

Dunbar, R.I.M. 1977. Feeding ecology of gelada baboons: Preliminary report. In: T.H. Clutton-Brock editor. Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes. pp.251-273. Academic Press, London.

Durham, W.H. Sexual differences in visual threat displays of West African Vervets. Primates 29:91-101.

Eisenberg, J.F., N.A. Muckenhirn and R. Rudran. 1972. The relation between ecology and social structure in primates. Science 176:863-874.

Fairbanks L.A. Interindvidual distance in relation to age-sex class and behaviour in Cercopithecus aethiops sabaeus: Comparison of field and enclosure. Unpublished Manuscript.

Fairbanks, L.A. and J. Bird. 1978. Ecological correlates of interindividual distance in the St. Kitts Vervet. (Cercopithecus aethiops sabaeus). Primates 19:605-614.

Galat, G. and A. Galat-Luong. 1976. La colonisation de la mangrove par Cercopithecus aethiops sabaeus au Senegal. Terr. Vie. 30:3-30.

Galat, G. and A. Galat-Luong. 1977. Demography et regine alimentaire d'une troupe of Cercopithecus aethiops sabaeus au habitat marginal au nord Senegal. Terr. Vie. 31:557-577.

Gartlan, J.S. 1968. Structure and function in primate society. Folia Primatol. 8:89-120.

Gartlan, J.S. 1972. Influence of phylogeny and ecology on variation in the group organization of primates. Symp 4th Int. Congr. Primatol. 1:88-101.

Gartlan, J.S. and C.K. Brain. 1968. Ecology and social variability in Cercopithecus aethiops and Cercopithecus mitis. In: P.Jay ed. Primates. Studies in Adaption and Variability. pp. 253-292. Holt, Rinehart and Winston, New York.

Gaulin, S.J.C. 1979. A Jarmen/Bell Model of primate feeding niches. Human Ecology 7:1-20.

Goss-Custard, J.D., R.I.M. Dunbar and F.P.G. Aldrich-Blake. 1972. Survival, mating and rearing strategies in the evolution of primate social structure. Folia Primatol. 17:1-19.

Gould, S.J. 1981. The mismeasure of man. W.W. Norton and Co., New York.

Gouzoules, S.M. 1981. Social relationships of adult female Japanese Monkeys (Macaca fuscata) Ph.D. University of Chicago.

Gysel, L.W. and L.J. Lyon. 1980. Habitat analysis and evalution. In: S.D. Schemnitz editor. Wildlife Management Techniques Manual. pp. 305-327. 4th edition. The Wildlife society, Washington.

Hall, K.R.L. 1963. Some problems in the analysis of comparison of monkey and ape behaviour. In: S.L. Washburn ed. Classification and Human Evolution. Aldine Press, Chicago.

Hall, K.R.L. and J.S. Gartlan. 1965. Ecology and behaviour of the vervet moneky, Cercopithecus aethiops, Lolui Island, Lake Victoria. Proc. Zool. Soc. Lond. 145:37-56.

Harris, R.J. 1975. A primer of multivariate statistics. Academic Press, New York.

Harthorn, G.S. 1978. the treefalls and tropical forest dynamics. In: J.C. Doyle ed.

Tropical Trees As Living Systems. Pp. 234-251. Academic Press, New York.

Harvey, P.H. 1977. The measurement of dietic diversity. In: T.H. Clutton-Brock editor. Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes. pp. 591-594. Academic Press, London.

Henzi, S.P. and J.W. Lucas. 1980. Observations on the inter-troop movement of adult vervet monkeys (Cercopithecus aethiops). Folia Primatol. 33:220-235.

Hladik, C.M. 1975. Ecology, diet and social patterning in Old and New world primates. In: R.H. Tuttle editor. Socioecology and Psychology of Primates. pp. 3-35. Moulton, Paris.

Hladik, C.M. 1977. A comparative study of the feeding strategy of two sympatric species of Leaf Monkeys : Presbytis senex and Presbytic entellus. In: T.H. Clutton-Brock editor. Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes. pp. 481-501. Academic Press, London.

Itani, J. 1977. Evolution of primate social structure. J. Human Evol. 6:235-243.

Iwamoto, T. 1974. Food availability as a limiting factor in population density of the two primates Japanese Monkey and Gelada Baboon. Primates 15:241-262.

Janzen, D.H. 1970. Herbivores and the number of tree species in tropical forests. Amer. Natur. 104:501-528.

Janzen, D.H. 1978. New horizons in the biology of plant defences. In: G.A. Rosenthal and D.H. Jansen eds. Herbivores: Their Interactions with Secondary Plant Metabolites. pp.539-566. Academic Press, London.

Jorde, L.B. and J.N. Spuhler. A statistical analysis of selected aspects of primate demography, ecology and social behaviour. J. Anthro. Res. 30:199-223.

Kano, J. 1978. A pilot study on the ecology of pygmy chimpanzees Pan paniscus. In D.A. Hamburg and E.D. McCown (eds). The Great Apes. pp.123-136. Benjamin/Cummings Pub. Co., London. Kavanagh, M. 1978. The diet and feeding behaviour of Cercopithecus aethiops tantalus. Folia Primatol. 30:30-63.

Kavanagh, M. 1978b. Monkey's new life in the forest. New Scient. 77:515-517.

Kavanagh, M. 1980a. Invasion of the forest by an African savannah monkey: Behavioural adaptations. Behaviour 73:238-260.

Kavanagh, M. 1980b. Selective pressures and socio-ecology of a West African Cercopithecine monkey. Tropical Ecology and Development. pp.377-382.

Kavanagh, M. 1981. Variable territoriality among Tantalus Monkeys in Cameroon. Folia Primatol. 36:76-98.

Klein, L.L. and D.J. Klein, 1975. Social and ecological contrasts between four taxe of neotropical primates. In: R.H. Tuttle editor. Socioecology and Psychology of Primates. pp. 59-83. Mouton Pub. The Hague.

Krebs, J.R. 1978a. Optimal foraging: Decision rules for predators. In: J.R. Krebs and N.B. Davis editors. Behavioural Ecology. pp. 23-63. Sinauer Associates, Inc. Pub. Sunderland.

Krebs, C. 1978. Ecology: The experimental analysis of distribution and abundance. Harper and Row Publishers, New York.

Kummer, H. 1967. Dimensions of a comparative biology of primate groups. Amer. J. Phys. Anthrop. 27:357-366.

Kummer, H. 1968. Social organization of the Hamadryas Baboon. University of Chicago Press. Chicago.

Kummer, H. 1971. Primate Societies. Aldine-Atherton, Inc., Chicago.

Loizos, C. 1965. Play in Mammals. Symp. Zool. Soc. Lond. 18:1-19.

Lancaster, J.B. 1971. Play mothering: The relations between juvenile and young infants amoung free-ranging vervet monkeys (Cercopithecus aethiops). Folia Primatol. 15:161-182.

McGuire, M. 1974. The St. Kitts Vervet. Contrib. Primat. 1:1-199.

Milton, K. 1980. The foraging stategy of Howler Monkeys. Columbia University Press, New York.

Moreno-Black, G. and W.R. Maples. 1977. Differential habitat utilization of four Cercopithecidae in a Kenyan forest. Folia Primatol. 27:85-107.

Nie, N.H., C.H. Hill, J.G. Jenkins, K. Steinbrenner and D.H. Bent. 1975. SPSS. Statistical Package For The Social Sciences. 2nd edition. McGraw-Hill Book

Company, New York.

Nishida, T. 1968. The social group of wild chimpanzee in Mahali Mountain. Primate 9:167-224.

Partridge, L. 1978. Habitat Selection. In: J.R. Krebs and N.B. Davis editors. Behavioural Ecology. pp. 351-376. Sinauer Associates, Inc. Pub. Sunderland.

Poirer, F.E. 1972. The St. Kitts Green Monkey (Cercopithecus aethiops sabaeus) ecology, population dynamics and selected behavioural traits. Folia Primatol. 17:20-55.

Redican, W.K. 1975. Facial expressions in nohuman primates. Primate Behav. 4:104-194.

Rowell T.E. 1971. Organization of caged groups of Cercopithecus monkeys. Anim. Behav. 19:625-645.

Rowell, T.E. 1972. Social behaviour of monkeys. Penguin Books, Baltimore.

Sade, D.S. and R.W. Hildrech. 1965. Notes on the Green Monkey (Cercopithecus aethiops sabaeus) on St. Kitts, West Indies. Carib. J. Sci. 5:67-79.

Seber, G.A.F. 1982. The estimation of animal abundance. 2nd edition. MacMillan Pub. Co., Inc., New York.

Skinner, J.D. and C.P. Skinner. 1974. Predation on the cattle egret (Bulbulcus ibis) and masked weaver (Ploceus velatus) by the vervet monkey (Cercopithecus aethiops). S. Afr. J. Sci. 70:157-158.

Spuhler, J.N. and L.B. Jorde. 1975. Primate phylogeny, ecology and social behaviour. J. Anthro Res. 31:376-405.

Struhsaker, T.T. 1967a. Ecology of vervet monkeys (Cercopithecus aethiops) in Masai-Amboseli Game Reserve, Kenya. Ecology 48:891-904.

Struhsaker, T.T. 1967b. Behaviour of vervet monkey(Cercopithecus aethiops) Cal. U. Pub. Zool. 82:1-74.

Struhsaker, T.T. 1967c. Social structure among vervet monkeys. Behaviour 29:83-121.

Struhsaker, T.T. 1967d. Behaviour of vervet monkeys and other Cercopithecines. Science 56:1197-1203.

Struhsaker, T.T. 1969. Correlates of the ecology and social organization among

African cercopithecines. Folia. Primatol. 11:80–118.

Struhsaker, T.T. 1978. Food habits of five monkey species in Kibale Forest, Uganda. In: D.J. Chivers and J. Herberts editors. Recent Advances in Primatology. Academic Press, London.

Struhsaker, T.T. and L. Leland. 1979. Socioecology of five sympatric monkey species in the Kibale forest, Uganda. Advances in the study of Behaviour. 9:159–227.

Tollman, S.G. and J.R.E. Simpson. 1975. An examination of the apparent 'wasteful' feeding behaviour in Cercopithecus aethiops : A new perspective? J. Behav. Sci. 2:99–114.

Van Hooff, J.A.R.A.M. The facial displays of the Catarrhine monkeys and apes. In D.M. Morris. (ed.). Primate Ethology. Alpine Press. Chicago.

Webb, L.J., J.G. Tracey and W.T. Willaims. 1972. Regeneration and pattern in subtropical rainforest. Ecology 60:675–696.

Whitmore, T.C. 1978. Gaps in the forest canopy. In: J.C. Doyle ed. Tropical Trees as Living systems. Academic Press, London.

Wrangham, R.W. 1981. Drinking competition in vervet monkeys. Anim. Behav. 29:904–910.

VIII. Appendix 1 : Ethogram of Vervet Behaviour

FEEDING

An animal was considered to be feeding when it was reaching for potential food items, harvesting them, transferring them to its mouth or chewing on the food. Times when the animal was moving between feeding sites, or during periods of inactivity in between feeding bouts, was not be considered within this category.

DRINKING

Vervets have been described to drink in two fashions. The first and most common way is drinking from water holes or rain pools by flexing their arms and legs and lowering themselves to the water (Struhsaker, 1967b). The second method involves drinking from water that is caught in the V formed from the meeting of tree branches. In this case the vervets either lowered their mouths to the water or dipped their fingers into the water and then licked the water from their fingers. Both of these methods were lumped under the category of drinking.

ELIMINATION

Both urination and defecation have been noted to occur when the individuals were in normal standing or sitting positions, on the ground and in the trees (Struhsaker, 1967b). Thus, elimination can only be considered to have occurred if the actual waste by products are seen being passed. The assessment of this behaviour was aided by the fact all other activities ceased whenever an individual is involved in either urination or defecation.

LOCOMOTION

No distinction was made between the two principle fashions of locomotion; walk and gallop. The description of these two behaviours is available in Struhsaker(1967b). This category included any movement that occurs between local feeding sites, but did not include the movements commonly noted in play and occasionally in certain types of agonistic encounters such as the chase and false chase (noted below).

RESTING

An animal was considered to be resting when it was obviously not engaged in any other activity. Struhsaker (1967b) describes the body positions that were assumed by vervets when resting as extremely variable but notes that the most common position is for the animal to rest on its ischial callosites.

GROOMING

This behaviour category was subdivided into two subcategories; self groom and allo-groom. Grooming has been defined as the process of searching through one's own or another animals fur and removing extraneous material from the pelage or skin with the fingers, lips or teeth (Bramblett 1980).

A) Self grooming or self cleaning

This behaviour was considered to be a non-social behaviour, involving movement patterns directed at the examination and cleaning of one's own pelage.

B) Allo-grooming

Allogrooming is a social behaviour involving one individual grooming another. This behaviour was variable, it involved the groomer brushing the pelage of the groomee with its hands and appearing to remove foreign particles with either the hands, lips or teeth. Virtually every part of the body can be groomed.

C)Solicite grooming

Often prior to a grooming bout, one individual invited or solicated a second individual to groom. This was commonly done by presenting the part of the body that the individual desires to be groomed. Lip smacking and teeth chattering often accompanied the presentation (see below). For the purpose of analyses all three of these grooming subcategories were lumped into one category.

AVOID

Avoid was used to describe the behaviour of a subordinate individual that moved out of the way of a more dominant individual. The dominant individual tended to be relatively passive and primarily ignores the individual. Neither the

vacated space nor the object that occurred in that space were taken by the dominant animal (Bramblett, 1980). This behaviour involves two parties and in order to understand the implications of the encounter the direction of the encounter was recorded.

SUPPLANT

This behaviour differs from avoid in that it involves the forceful displacement of an individual in which the dominant individual acquires the subordinate animals possession or space. Here again it is essential to record the direction of the encounter and the participants.

ATTENTION

When ever an animal appeared to be in a state of vigilance and was observing the environment it was considered to be exhibiting this behaviour.

YAWNING

Yawning is considered indicative of a state of tiredness, however, it may also express a state of unrest or anxiety (Rowell, 1971). Only those instances in which the animal was viewed to be expressing a state of unrest was this behaviour recorded.

PLAY

The patterns of behaviour involved in play are extremely variable, however in most situations it is apparent to the observer when play behaviour is occurring. Since two studies (Struhsaker, 1967b; McGuire, 1974) have noted that solitary play was extremely rare in feral vervets was not considered.

A) Play Face

This facial expression is often noted to preceed and accompany play behaviour. It is also called the "relaxed open mouth face" by Van Hooff (1967). In the play face, the mouth is widely opened and the corners of the mouth are slightly retracted (Redican, 1975). The upper incisors and canines may or may not be exposed (Struhsaker, 1967b). The observation of the play face expression was used in two fashions: firstly, if the individual expressing this facial expression was engaged in activities that could potentially be considered playful but where some confusion exists, it was used to verify whether or not

the situation should be considered playful or not. Secondly, if it was seen to be exchanged between two individuals but no behaviour that could be considered to be play was seen or if it preceeded a bout of play, then the play face was considered to have been used to solicite play.

SEXUAL BEHAVIOUR

The frequency of sexual behaviour can be measured by examining the rate of occurrence of the various behaviours that are included in sexual behaviour in general.

A) Mounting

Mounting was recorded whenever an individual assumed the copulatory position over another individual. In a typical heterosexual mounting the male assumes the copulatory position by grabbing and holding onto the hips of the female with his hands and grasps the back of her calves with his feet. An animal can assume the copulatory position in either a reproductive or an approach-dominance context (Bramblett, 1980). These two functions of mounting can be distinguished, for non-reproductive mounting often lacks the leg clasping with the feet and is typically characterized by relatively brief encounters. Also non-reproductive mounting lacks the thrusting characteristic of reproductive mounting and always lacks the ejactulatory pause (Struhsaker, 1967b).

B) Presenting

Since female vervet monkeys in estrus show no physical signs which demonstrate their condition, they demonstrate receptivity by behavioural means, such as presenting. This involves the female orientating her posterior quarters in the direction of a male. The female is described to sometimes glances over her shoulder in the direction of the male (Struhsaker 1967b). This behaviour was considered to be the female's way of soliciting the male for sexual attention.

C) Hip Touch (Bramblett, 1980) or Grabbing Hips (Struhsaker, 1967b)

This behaviour involves the touching, patting or grasping of an individuals hips. When the interaction involved a male touching the hips of a female it was often followed by the female assuming the appropriate reproductive position, if she was in a receptive state. The hip touch was also noted to occur between

members of the same sex. In heterosexual situations it was viewed that the male was preforming this behaviour in attempt to assess whether or not the female was receptive to him.

AFFILIATIVE

a)Lipsmack

Lipsmacking involves the rapid opening and closing of the mouth often resulting in an audible smacking sound. This display often involved one of several variations, such as wetting the lips,(Bramblett, 1980), sticking the tongue out between smacks, or the chattering of the teeth (Struhsaker, 1967b). Lipsmacking is thought to represent the nonaggressive tendencies of the preformer, as well as, familiarity. It is strongly associated with grooming. (Bramblett 1980).

b)Muzzle (Bramblett, 1980)

(also called Muzzle-Muzzle Struhsaker, 1967b, Nose-Mouth Rowell, 1971)

This behaviour involves one individual placing its nose very near to the mouth of another individual. Muzzle contact commonly preceded grooming, and occurred frequently in both juvenile and adult age groups. It was also often observed as an exploratory behaviour noted during feeding. The muzzle behaviour appears to be neither submissive nor aggressive and is probably best labelled as social or exploratory (Bramblett, 1980).

c)Embrace

An embrace involves one animal placing its forelimbs around another. Either the animal can embrace from behind or from infront of the other individual. An enbrace is considered to be a non-hostile greeting between two individuals. It often preceded by grooming.

These three behaviours was considered to express the non aggressive nature of the motivations of the preformer. They seem to either invite

non-aggressive behaviours, such as grooming, or they allow the performer to do non-aggressive behaviours without receiving aggressive reprisals that could have resulted because the receiver was confused about the intentions of the preformer.

AGONISTIC BEHAVIOURS

Aggressive Threat

a)Headbob.

This behaviour involves bouncing the head in an up and down fashion (Durham, 1978). The extent of the movement can be very small or it can be quite extensive. The intensity and extent of movement of the head may indicate the intensity of the threat. Struhsaker (1967b) describes a similar behaviour which he terms "jerking of the head".

b)Body Bounce.

Also called "jerking of the body" by Struhsaker (1967b). This behaviour seems to be an extension of the head bob display, and to express a more hostile threat. The body bounce was more likely to lead into an attack than is the head bob (Struhsaker, 1967b). This behaviour involved the up and down and back and forth movements of the forequarters and the head of the threatening individual. It was often accompanied by the threatening animal staring directly at the recipient of the display.

c)Open-Mouth Threat

In this display the mouth is opened, the corners of the mouth are brought forward and the lips are formed into a circular aperture (Redican, 1975). The teeth are usually not visable for they are covered by the lips, however the canines may be exposed. This threat face is often given names such as the "staring open mouth threat" (Van Hooff, 1967) or the "canine display" (Durham, 1978). The open-mouth threat was considered to be an aggressive threat and was often given in conjunction with a stare or a lid (see below).

d)Bite

This behaviour was an actual bite, where the teeth were utilized. Fear or pain reactions were expressed by the recipent. This category does not include the mouthing of the fur where the teeth are not used which was common in play. The function of the bite was considered to be either aggressive or punitive.

e)Cuff

This is an open handed slap, usually directed towards the head or the forequarters of the recipent . It functions as a mild attack or rebuff (Bramblett, 1980). The cuff is also termed "Slapping" (Struhsaker, 1967b) and "Hitting" (Rowell, 1971).

f)Grabbing

Grabbing involves the grasping and pulling of the hair of another individual. The more preferred site to grab is the hair of the head or scalp (Bramblett, 1980). Like the cuff, grabbing was viewed to function as a punitive act or as a mild aggressive attack.

g)Branch Shaking Display

This display was highly variable but usually involved the grasping of a branch with the forehands and rapidly jerking it up and down and back and forth. This display was commonly directed at an individual and functions as an aggressive threat. The branch shaking display may be very similar in both function and form to the "body bounce".

h)Chase and Attack

This involved the aggressor moving at maximum speed towards the recipient, who either met the charge or more commonly fled. While rapidly withdrawing, the recipient often glanced over its shoulder and gave submissive vocalization (Struhsaker, 1967b).

McGuire (1974) states the the Red-White and Blue Display described by Struhsaker (1967b) is not exhibited by the St. Kitts vervets. Potentially some subunits of the display still are exhibited. For example, McGuire (1974) describes a variant of encircling in which the animal only partially encircles the animal and

veers off in another direction. No contextual information was presented that would suggest any function for such a display.

i)Stare

A stare is described as an unmoving gaze that is directed towards an individual for a relatively long period of time, from 3 to 5 seconds (Redican, 1975; Struhsaker, 1967b). The stare seems to function as a threat gesture which depending upon the accompaning behavioural patterns can be either defensive or aggressive.

j)Lid

The lid involves the retraction of the scalp and eyebrows, as well as the lowering of the lightly colored eyelids. Struhsaker (1967b) labels this behaviour as "exposure of the eyelids" and views that it represents a threat that can function in a defensive manner if given from a crouched position, or in an aggressive manner if given from a "confident" position

k)False Chase

The chaser has a slow, hesitant, jerky stride in which the legs are kept partially flexed throughout the stride. This was countered by the recipent of the false chase which has a confident stride. The chaser never catches the chasee, and the chase is normally terminated when the chasee stops and turns around and stares at its pursuer. The function of this display is not clearly understood, however it is viewed that the chaser is always the subordinate individual of the pair.

l)Crouch

In a crouch the animal flexes its arms and legs so as to bring its body close to the substrate. The head is also lowered towards the ground and the tail is held low. Struhsaker (1967b) found that crouching seldom gave rise to an attack and he interpreted this to mean that the crouch was a defensive threat.

m)Rapid Glancing

This gesture was exhibited by individuals that were the potential recipients of aggression. It involved the glancing away from and towards the potential attacker. Glancing can function to solicite aid, from other individuals against the

attacker as well as possibly functioning to indicate subordination.

n\Gape

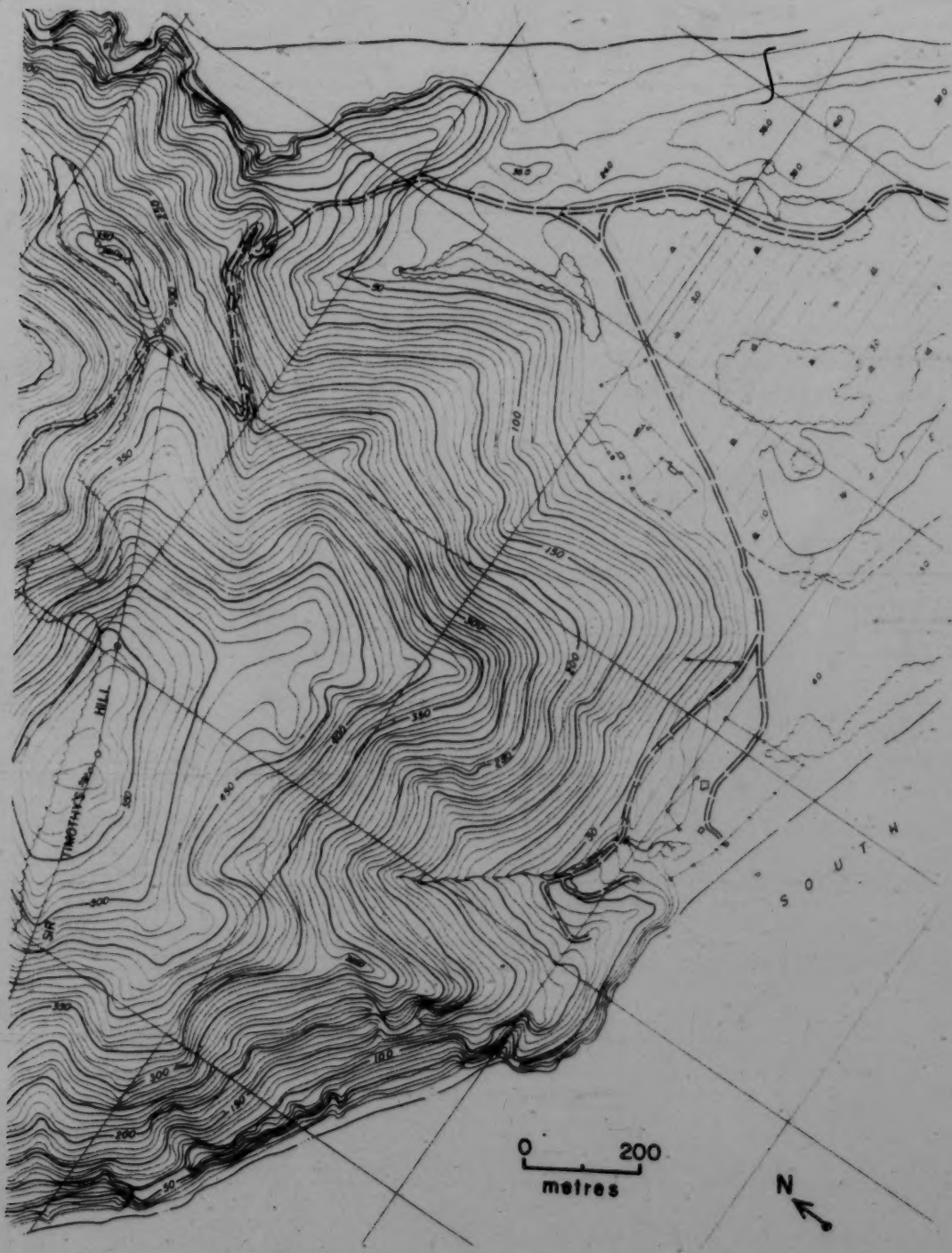
In order to make the gape expression an animal opens its mouth and thrusts its lower jaw forward, tenses its lips to cover its teeth and stares at the recipient. Frequently the animals gave a lid while it was in a crouch position. Struhsaker (1967b) viewed that the function of a gape was as a defensive threat.

n\Grimace

In the grimace the mouth is held open and the corner of the mouth and lips are held back exposing the unclenched teeth. The grimace has been described to appear in three distinct contexts: the first situation involves the grimace being displayed by a individual that is the potential recipient of an overt aggressive act, such as an attack. In this instance it seems to function as a defensive threat (Struhsaker, 1967b). In the second situation the grimace is commonly given by a male as a display during copulation (Redican, 1975). This function has however apparently not been reported for vervets. In the third situation the grimace is given in the context of greeting. It seems to serve to allow the sender to approach another animal with the minimum level of aggression. No attempt was made to distinguish between the three contexts of the grimace display. Redican (1975) distinguishes a second form of the grimace, the "Open Mouth Grimace". The facial movements are similar to the grimace, except that the mouth is opened relatively wide. It seemed to be given in the same context, but seemed to involve components of a threat as well as the grimace.

VOCALIZATIONS

No Attempt was made to record the different types of vocalizations.



Appendix 2 Study area of the St. Kitts vervets.

APPENDIX 3 : THE PLANTS FOUND ON SIR TIMOTHY HILL, ST. KITTS

SCIENTIFIC NAME	COMMON NAME
Plumeria sp.	Green Wax Tree
Croton balsamifera	Limp Tree
Lantana involucrata	Sage
Stachytarpheta jamaicensis	Strawberry
Lantana sp.	Sage
Acacia farnesiana	Acacia/casha
	Olive Tree
	Tri-Olive Tree
Citharexylum caudatum	Poplar Bush
Calotropis procera	Olive Jade
	Small Poplar Bush
Randia aculeta	Spiny Holly
Krugiodendron ferreum	Pear Leaf Tree
Tabebuia pallida	Dragon Olive
Croton balsamifera	Vein Leaf Crawler
Lantana sp.	Glossy Sage
	Glossy Vine
	Four Leaf Tumble Weed
Coccoloba uvefera	Seagrape
Caesalpine bonduc	Seagrape Vine
	Seagrape Bush
	Seagrape Cockspur
Rhizophera mangle	Mangrove
	Mangrove Grass
	Small succulent
	Large succulent
Laguncularia racemosa	Marsh Tree
	Purple Limp Bush
	Red Fringe Tree
Krameria ixina	Spiny Ball Bush
	Serrated Olive
Melocactus intortus	Turks Head Cactus
	Slope Vine
Agave americana	Century Plant
Bursera simaruba	Gumbo Limbo
Bourreria succulenta	Asparagus Tree
Opuntia megacantha	Prickly Pear Cactus
Zebrina pendula	Wandering Jew
	Gut Tri-Wax Vine
Capparis flexvosa	Gut Bean Tree
	Tri-Limp Vine
	Eaten Tree
Piscardia piscipula	Wingfruit Tree
Celtis iguanea	Cockspur
	Small Leaf Tree
	Bi-Wax Tree
Catharanthus roseus	Purple Flower Plant
	Plateau Vine
	Plateau Green Tree
Clerodendrum aculeatum	Plateau Olive Vine
Cassia sp.	Mottle Bark Tree
	Clover Tree
	Giant Poplar
	Plateau Dark Mottled

Cephalocereua royenii	Pole Cactus
Lantana sp.	Limpy Birch
Rauwolfia nitida	Long Leaf Tree
	Small Serrated
Cordia sp.	Even Leaved Tree
Jatropha gossyiifolia	Inedible Shrub
Cordia obliqua	Clammy Cherry Tree
Hippomane mancinella	Mancineal
	Pasture Tree
Terminalia catappa	Almond Tree
Cocos nucifera	Coconut Tree